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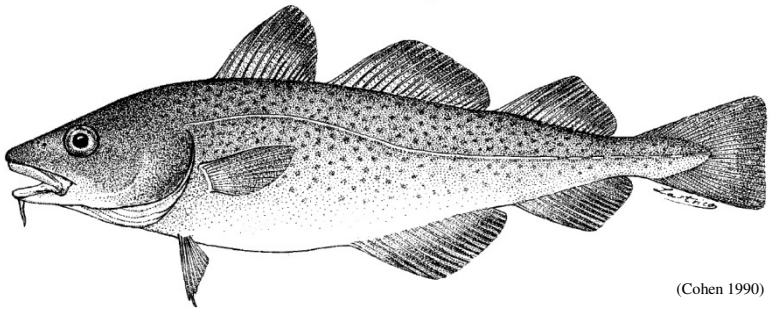
Trophic dynamics of Baltic fish species after the 2014 Major Baltic Inflow event



(Cohen 1990)

submitted by
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LIST OF ABBREVIATIONS

δ	delta
AB	Arkona Basin
BB	Bornholm Basin
C	carbon
e.g.	for example
F	female
GB	Gotland Basin
GD	Gdansk Deep
ICES	International Council for the Exploration of the Sea
i.e.	in other words
JFT	“Jungfischtrawl”; pelagic trawl net of 0.5 cm mesh size
K_n	relative condition factor
M	male
N	nitrogen
psu	practical salinity unit
RV	research vessel
S	sulphur
SCA	stomach content analysis
SD	“subdivision”; ICES spatial management unit
sd	standard deviation
SEAc	standard ellipse area for small sample sizes
SIA	stable isotope analysis
sp.	species
TL	total length
vs.	versus

ABSTRACT

The Baltic Sea is among the ecosystems most affected by global and regional environmental perturbations worldwide, including the drastic expansion of hypoxic areas in recent decades. This has had direct effects on the biota living in the Baltic Sea, such as the reduction of benthic invertebrates, which also represent a food resource for fish communities. In December 2014, the occurrence of a Major Baltic Inflow (MBI) event transporting large amounts of saline, oxygen rich North Sea water to the deep layers of the Baltic Sea may have led to trend reversal in the availability of benthic resources. This raises the question how major fluctuations in the availability of benthic versus pelagic prey resources have affected Baltic fish species. In particular, this is in relation to the commercially and ecologically important fish species Baltic cod (*Gadus morhua*), which has experienced a strong decline in body condition over the period of extending hypoxia. In this context, better characterisation of benthic versus pelagic feeding by cod and the characterisation of feeding interactions in Baltic fish communities after the 2014 MBI are urgently needed. To address this knowledge gap, I assessed the trophic dynamics of Baltic cod and 12 other fish species in April 2016, using stable isotope analysis (SIA) of carbon (C), nitrogen (N) and sulphur (S). My particular focus lay on ontogenetic patterns of benthic versus pelagic feeding in cod, and on the potential for interspecific competition in three different fish groups, the piscivore predators cod and whiting (*Merlangius merlangus*), the pelagic fishes herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and three-spined stickleback (*Gasterosteus aculeatus*), and the flatfishes dab (*Limanda limanda*), flounder (*Platichthys flesus*) and plaice (*Pleuronectes platessa*). In total, 296 samples of 17 species from 4 basins and 14 sites were analysed, to ensure a high spatial resolution of the spatio-temporally variable Baltic environment. Results show (1) the overall trophic structure of the community, (2) an ontogenetic diet shift from benthic to pelagic prey in cod, (3) a positive trend of cod condition with an increasing benthos proportion in the diet, (4) a surprisingly low isotopic niche overlap for cod and whiting, (5) little evidence for interspecific competition between the pelagic fishes, and (6) a strong potential for competition within the flatfish community. Sulphur data provided the most informative insights, especially for the assessment of benthic-pelagic diet shifts in this study. This work offers valuable insights into the trophic dynamics of Baltic fish species including non-commercial species that are not routinely assessed with stomach content analyses. Thus, it demonstrates the potential of SIA to routinely assess the overall Baltic food web structure in a relatively convenient and logistically easy way, demonstrated by the spatially resolved data set for both commercial and non-commercial fish species provided by a single research cruise.

1. INTRODUCTION

Marine ecosystems are increasingly affected by environmental changes in the context of global and local anthropogenic impacts (Walther et al. 2002, Doney et al. 2011). This includes alterations in community structure e.g. due to geographic range shifts of species (Sorte et al. 2010), arrival of non-indigenous species (Ruiz et al. 1997) and disappearance of keystone species due to environmental perturbations (Scheffer et al. 2001). The ecological effects on the ecosystem include changes in species interactions, such as competition and predation (Joël et al. 2007), and on the species level, dietary shifts (Österblom et al. 2007). Ecology therefore more than ever needs to integrate both the biological characteristics of species and systems, and the environmental properties of the ecosystem.

The Baltic Sea (Figure 1) is one example where these environmental changes are occurring even faster than on a global average (Reusch et al. 2018). It is a large, semi-enclosed brackish sea (Rudstam et al. 1994) with a surface area of 415.000 km^2 and a volume of 21.700 km^3 (Jansson 2002) that is characterised by naturally high environmental fluctuations over time, as inflow events of highly saline and oxygen rich water from the North Sea only occur infrequently (Matthäus et al. 2008, Mohrholz et al. 2015). Furthermore, there is a strong spatial gradient ranging from near marine conditions in the western Baltic Sea (>15 PSU in the Kattegat) to brackish and even freshwater conditions in the eastern Baltic Sea (<3 PSU in the Bothnian Bay) (Carlsson 1997). The geography and hydrography of the Baltic Sea make this ecosystem particularly vulnerable to increasing anthropogenic and climate pressures such as ocean warming, eutrophication, acidification, deoxygenation, toxic contamination and the introduction of non-indigenous species (Reusch et al. 2018).

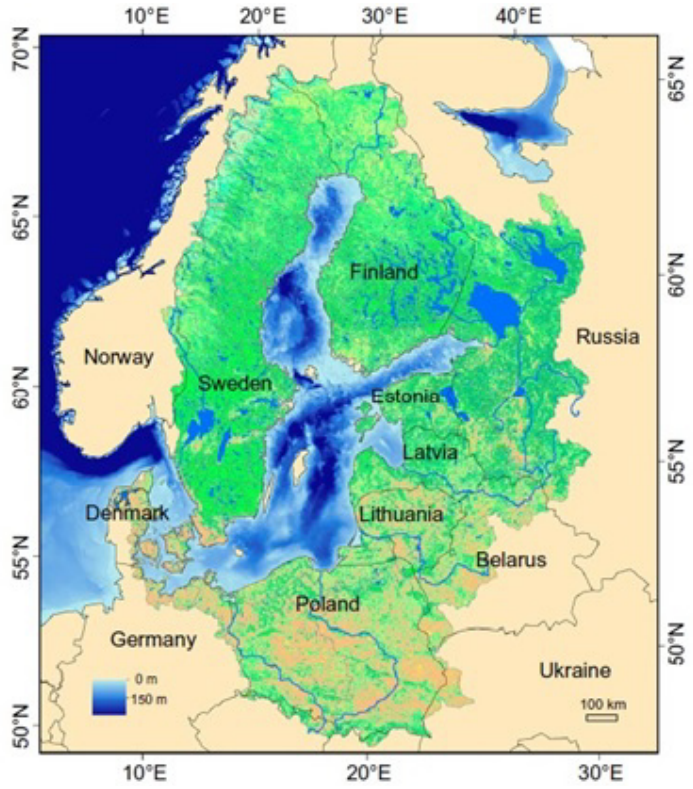

Figure 1. The Baltic Sea and its neighbouring countries and catchment area (Reusch et al. 2018).

In recent decades, areas of anoxia and hypoxia have extended in the Baltic Sea due to a combination of lacking or infrequent Major Baltic Inflow (MBI) events from the North Sea

(Mohrholz et al. 2015), eutrophication and warming. This trend was reversed in December 2014, when the third strongest MBI event on record interrupted the 10-year stagnation period (Mohrholz et al. 2015). As a consequence, the Bornholm and Gotland Basin deep water conditions changed from anoxic to oxic (Mohrholz et al. 2015), and the 2014 MBI event may thus have the potential to have a crucial impact not only on the environmental conditions in the Baltic Sea, but on the entire Baltic ecosystem and its species (Mohrholz et al. 2015).

The Baltic Sea is a species-poor ecosystem, yet highly productive and important with regard to fisheries (Svedäng & Hornborg 2014). Compared to fully marine seas, it harbours a relatively small fish community within a rather simple food web consisting of fewer components (Figure 2). However, the ecological community structureis much more complex when looking at the food web components in detail.

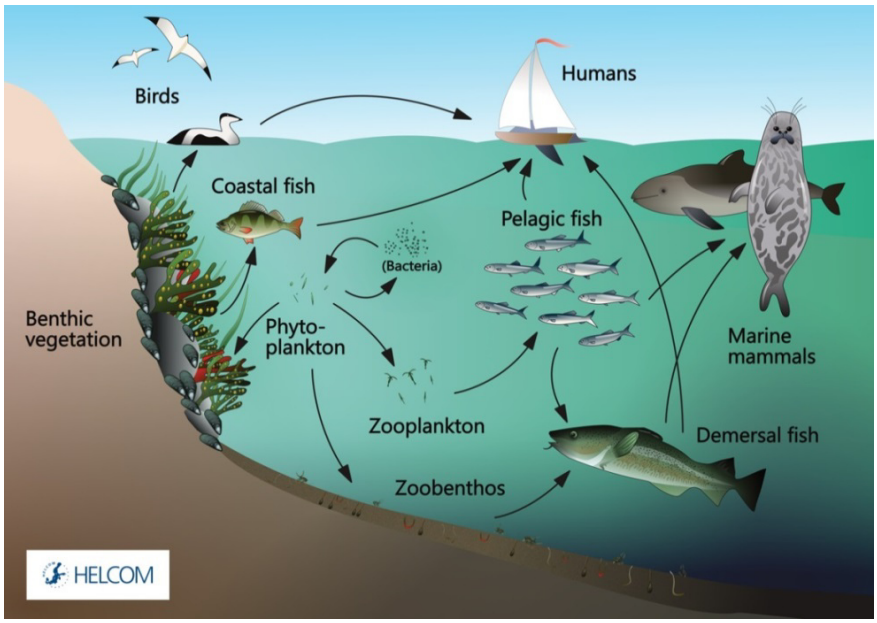

Figure 2. A schematic, simplified illustration of the Baltic Sea food web structure (HELCOM 2017).

Baltic cod (*Gadus morhua*) is the commercially and ecologically most important fish species in the Baltic Sea (Svedäng & Hornborg 2014). It is a benthopelagic top predator in the Baltic ecosystem and shapes the food web community via top-down control and resulting trophic cascades (Rudstam et al. 1994, Möllmann et al. 2009). At the same time, its population size and ecology are closely linked to the given environmental characteristics of the Baltic Sea (Casini et al. 2016). Previous research has shown that the expansion of anoxic and hypoxic areas negatively affects the body condition of cod (Eero et al. 2015, Casini et al. 2016). It is still unclear however, whether this is due to crowding and competition in shallower, oxygenated areas, direct physiological effects, or lack of benthic prey following

decline in benthos availability (Casini et al. 2016). Understanding the feeding ecology and body condition of Baltic cod is therefore complex, and is further complicated by the high spatial and temporal fluctuations in the Baltic Sea (Jansson 2002), which make it challenging to generalise conclusions obtained from studies with limited spatial scope.

Previous feeding ecology studies were mainly carried out through the traditional method of choice, stomach content analysis (SCA), where stomach contents are visually identified and their contribution to the diet (e.g. by weight) is measured (Hyslop 1980). These studies have shown that juvenile cod (total length TL <20cm) feed mainly on benthic invertebrates such as small crustaceans (*Mysis sp*., *Pontopoeira sp.*) (Bagge et al. 1994). The food composition then changes with increasing size of cod ("ontogenetic diet shift") to a mainly piscivore diet (Bagge et al. 1994). Preferable prey species for adult cod are primarily herring and sprat, but the diet is complemented by benthos such as *Saduria entomon* (Bagge et al. 1994).

Clupeids are not only an important food resource for cod, but also for whiting (*Merlangius merlangus*), the second main fish predator in the western Baltic Sea. In the past, whiting was only a visitor from the North Sea, but nowadays abundances of whiting have increased. Long-term data series of fish communities in the western Baltic Sea (GEOMAR unpublished) suggest that whiting may have established a self-sustaining population in the Baltic Sea. Similar to cod, whiting also undergoes an ontogenetic diet shift which generally takes place between 10 and 20 cm (Ross et al. 2013, Ross et al. 2016). It has been shown that clupeids make up to 90% of adult whiting's diet, yet little is known about its ecological role and predatory significance (Ross et al. 2013, Ross et al. 2016).

For these reasons, cod and whiting are very likely to compete for food in the western Baltic Sea (ICES subdivisions (SD) 22 – Kiel Bight, SD24 – Arkona Basin, SD25 – Bornholm Basin, Figure 6) and research is required to estimate the extent of their potential competition as well as the predatory significance of whiting in this area.

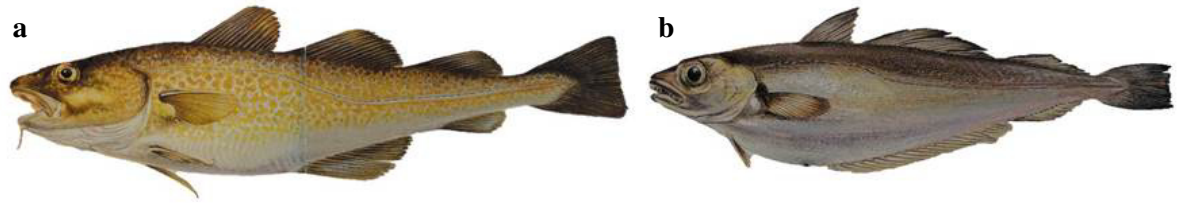

Figure 3. The piscivore predators (a) Baltic cod (*Gadus morhua*) and (b) whiting (*Merlangius merlangus*) (Muus et al. 1999).

The Baltic pelagic fish community is mainly constituted by the clupeids herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Heikinheimo 2011). Both fish species are of ecological and commercial importance in the Baltic Sea and have been subject of many

studies (Möllmann et al. 2004, Bernreuther 2007, Heikinheimo 2011, Danielsson et al. 2015). In recent years, the biomass of the three-spined stickleback (*Gasterosteus aculeatus*) has drastically increased in the Baltic Proper (including SD25 – Bornholm Basin) (Ljunggren et al. 2010) and it is assumed to represent a substantial part of the pelagic fish community in some areas of the Baltic (Jurvelius et al. 1996, Ljunggren et al. 2010). The species is planktivorous and mesopelagic like herring and sprat, and recent findings have shown that it may play a considerable role in the pelagic food web as a potential competitor for these two species (Jakubavičiūtė et al. 2017b), yet still very little is known about the competitive interactions in the pelagic community.

Figure 4. The pelagic fish species (a) herring (*Clupea harengus*), (b) sprat (*Sprattus sprattus*) and (c) three-spined stickleback (*Gasterosteus aculeatus*) (Muus et al. 1999).

In the demersal fish community, the flatfish species dab (*Limanda limanda*), flounder (*Platichthys flesus*), and plaice (*Pleuronectes platessa*) are particularly abundant. Flatfish are of ecological and commercial importance in the Baltic Sea, though they have been rarely assessed to date (Florin 2005). The highest biodiversity and abundance of flatfish is found in the western Baltic Sea (SD22 – Kiel Bight), where they mainly feed on benthic invertebrates such a molluscs and polychates, but also on small fishes such as sand eels (Arntz & Finger 1981). Even though Baltic flatfish species share similar prey items and are very likely to show interspecific competition, only little attention has been paid to their feeding ecology to date (Florin 2005).

Figure 5. The flatfish species (a) dab (*Limanda limanda*), (b) flounder (*Platichthys flesus*), and (c) plaice (*Pleuronectes platessa*) (Muus et al. 1999).

In summary, despite the fact that feeding ecology of many of the commercially important fish species of the Baltic has been assessed, far too little attention has been paid to their trophic dynamics such as interspecific competition. Additionally, very little is known about the commercially less important species. One major problem is that data are often not directly

comparable if datasets for different species were collected at different time points or locations. Moreover, the importance of benthic food for the top predator cod needs further evaluation to better understand the reasons behind the drastic decrease in its body condition.

Elucidating the trophic dynamics in the spatio-temporally variable environment of the Baltic Sea requires a method that allows a high spatio-temporal resolution. For this reason, stable isotope analysis (SIA) is the method of choice for the Baltic Sea ecosystem, but has surprisingly rarely been used to date (but see Gorokhova et al. 2005, Karlson et al. 2007, Almqvist et al. 2010, Mohm 2014, Danielsson et al. 2015). It reflects the assimilated diet over previous weeks to months (Hobson 1999), in contrast to SCA which only provides a "snapshot" in time, yet allowing a very detailed view of ingested prey taxa (Cocheret de la Morinière et al. 2003). As a consequence, SCA data are often temporally and spatially limited, making it difficult to detect general feeding patterns that result from time integration (Cocheret de la Morinière et al. 2003). Both methods have their specific advantages and disadvantages and provide complementary understanding of an animal's feeding ecology. While increasing spatio-temporal resolution in SCA studies is very labour intensive due to the high samples sizes that are required, one of the major strengths of SIA is the fact that lower sample sizes are needed, which are relatively easy to obtain.

Carbon (C), nitrogen (N) and sulphur (S) have been used to provide insights into trophic dynamics of animals, including patterns of ontogenetic diet shifts (Cocheret de la Morinière et al. 2003), spatial differences in feeding ecology (Hebert et al. 1999), migration patterns (Hansson et al. 1997), intraspecific feeding specialisation (Bertellotti et al. 2002), or interspecific competition (Kinney et al. 2011). All of these studies exploit the phrase "you are what you eat", i.e., the isotopic composition of an animal depends on the average composition of its prey, but with a biological offset ("fractionation") due to excretion and respiration, enabling us to draw biological conclusions from the stable isotope ratios observed in an animal's tissue (Peterson & Fry 1987) (Figure 1). Isotopes of C (mean trophic fractionation 0.4±1.3‰; Post 2002) are used to detect the organic carbon sources in the food web (Peterson & Fry 1987), allowing differentiation between pelagic and benthic prey sources. N isotopes are used to identify an organism's trophic position (Peterson & Fry 1987) because the isotopic ratio of N of a consumer is enriched by 3.4±1.0‰ relative to its diet (Post 2002). S isotopes represent a valuable complement to C isotopes because they make it possible to distinguish between living algae and sedimentary detritus as organic matter sources at the base of food webs, and thus, benthic versus pelagic feeding (Croisetière et al. 2009). The fractionation of S is assumed to be negligible (Peterson & Fry 1987).

A recent study that assessed the feeding ecology of Baltic fishes, including spatial differences in cod feeding ecology, the potential for competition with whiting, isotopic niche overlap in herring and sprat, and intraspecific plasticity in Baltic fish species, with the help of SIA underscored the potential of this method (Mohm 2014). At the same time, a comparison of C versus S stable isotopes as measure of benthic versus pelagic diet revealed that only S was suitable to reliably identify benthic diet use in the study system (Mohm 2014), highlighting that studies addressing this aspect should include systematic data on S. Priester (2018) used S isotope data of protein retrieved from archived cod otoliths to reconstruct Baltic cod feeding ecology over a timescale of 40 years with different environmental conditions including MBI events, and showed that benthos may even be available in years of stagnation which suggests fish migration to shallower, oxygenated areas. However, the study is only based on cod data from a single basin (SD25 – Bornholm Basin) with less sample size per year, lacking the needed spatial resolution and framework data for other species in the Baltic Sea.

Based on these studies, it becomes clear that framework data for a broad range of species along the environmental gradient in the Baltic Sea, based on SIA of C, N and S, is essential to better understand the feeding ecology of Baltic fish species.

This study provides such a dataset based on 296 samples of 17 species from 4 basins and 14 sites collected in April 2016. At the time of sampling, sufficient time for a reaction of benthic ecosystems to water masses that entered during the 2014 MBI event had passed. Samples were analysed with SIA of C, N and S. This high resolution data set extends a temporal data set, including C and N data from 2012 obtained in a pilot study and 2014 C and N data from Mohm (2014) (i.e., both pre-inflow), and represents a post-inflow data point.

The overall goal of the study is to elucidate the trophic dynamics of Baltic fish species based on SIA after the 2014 MBI event. My specific aims are to (1) describe the overall trophic structure of the whole community, (2) assess ontogenetic diet shifts and spatial differences in cod with a particular focus on benthic versus pelagic feeding, (3) evaluate body condition of cod and, in particular test the hypothesis that the relative condition factor (K_n) increases with increasing benthos proportion in the diet (as indicated by decreasing sulphur stable isotope ratios), (4) study the potential competition between cod and whiting, (5) investigate the potential of competitive interactions between the pelagic fish species herring, sprat and three-spined stickleback, and (6) examine the ecological niche overlap of the flatfish dab, flounder and plaice.

2. MATERIAL AND METHODS

2.1 Sampling

For this study, I used an existing sample set collected during a two week research cruise on RV ALKOR in April 2016 (cruise number AL476). The time of sampling marked 16 months after the 2014 MBI event. The sampling sites included SD22 - Kiel Bight (1 site), SD24 - Arkona Basin (4 sites), SD25 - Bornholm Basin (6 sites), and SD26 - Gdansk Deep (3 sites) (Figure 6). Fishing was done with a pelagic trawl net ("Jungfischtrawl", JFT) of 0.5 cm mesh size, which was run near the bottom for part of the time to accomplish sampling of both pelagic and benthic species. In total, 296 samples of 17 species from 14 sites were caught (Table 1).

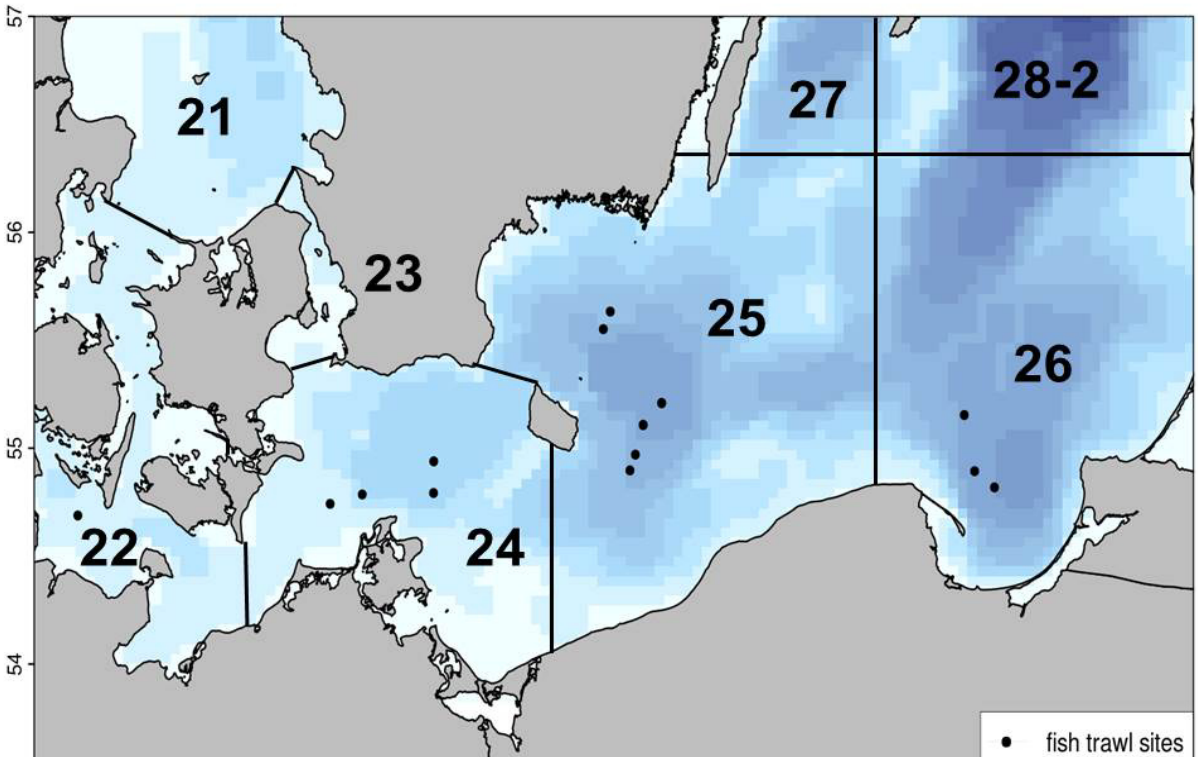

Figure 6. Sampling sites in ICES subdivisions (SD) covered during AL476 with pelagic trawls (JFT = "Jungfischtrawls"). Numbers on the y- and x-axis represent degrees N and E, respectively. Modified from Burkhard von Dewitz.

For each individual, the weight (nearest g), gutted weight (nearest g, only for cod) and total length (to the next lower half cm for herring and sprat; next lower cm for all other species) was measured. Dorsal white muscle tissue samples were then obtained using a biopsy punch (4mm; Stiefel; Durham, USA) or a scalpel. If present, skin and blood were removed to prevent contamination. All samples were immediately frozen at -20°C until further analysis. Here, I organised the sample set conserved in the freezers at GEOMAR, chose suitable sub-

samples for analysis, and connected single fish data on each individual with the physical samples that were used for stable isotope analysis.

Table 1. Sample sizes per ICES subdivision (SD) and species. SD22 – Kiel Bight, SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

Species	**ICES subdivision**				
	22	**24**	**25**	**26**	**Total**
Cod (*Gadus morhua*)	1	31	33	31	96
Whiting (*Merlangius merlangus*)	6	10	7		23
Herring (*Clupea harengus*)	10	10	10	10	40
Sprat (*Sprattus sprattus*)	10	9	10	9	38
Three-spined stickleback (*Gasterosteus aculeatus*)			9		9
Dab (*Limanda limanda*)	10	2			12
Flounder (*Platichthys flesus*)	10	5	9	10	34
Plaice (*Pleuronectes platessa*)	7	8			15
American plaice (*Hippoglossoides platessoides*)	1				1
Blue mussel (*Mytilus edulis*)		5			5
Common starfish (*Asterias rubens*)	5	5			10
Lumpfish (*Cyclopterus lumpus*)	2				2
Ocean quahog (*Arctica islandica*)	5				5
Red whelk (*Neptunea antiqua*)	3				3
Smelt (*Osmerus eperlanus*)			1		1
Spotted dragonet (*Callionymus maculatus*)	1				1
Turbot (*Scophthalmus maximus*)		1			1
Total	71	86	79	60	296

2.2 Stable isotope analysis

All samples were freeze-dried to constant mass (freeze-dryer alpha 1-1; Christ GmbH; Osterode am Harz, Germany) and then ground to fine powder using a mortar and pestle (75mm, 25ml; Carl Roth GmbH; Karlsruhe, Germany). 0.040-0.060 mg of powdered samples were weighted (MC 5 Micro Balance; Satorius; Göttingen, Germany) into cylindrical tin cups (3.2x4.0 mm; HEKAtech,; Wegberg, Germany). 0.25 mg of vanadium pentoxide (V_2O_5) was added as catalyst, to ensure the complete combustion of sulphur (Hansen et al. 2009). Folded tin cups were loaded into flat-bottomed 96-well tissue culture plates (Sarstedt; Nümbrecht, Germany). The internal standard hay (IS_{CNS}) was placed after every sixth sample to assess the quality of measurements (Hansen et al. 2009). Stable isotope analysis was carried out at GEOMAR (Helmholtz Centre for Ocean Research Kiel, Germany). $^{13}C/^{12}C$, $^{15}N/^{14}N$ and $^{34}S/^{32}S$ ratios were simultaneously measured using a highly sensitive elemental analyser (HSEA) interfaced to conventional isotope ratio mass spectrometer (EA-IRMS) (Hansen et al.

2009). Stable isotope ratios are expressed as delta values (δ), defined as the parts per thousand deviation (‰) from a standard material (Sherwood et al. 2007), using the formula

(1) $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$

where *X* is ^{13}C, ^{15}N or ^{34}S and *R* the corresponding isotope ratio ($^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$). Standards are Vienna PeeDee Belemnite (VPDB) for carbon, atmospheric nitrogen (N_2) for nitrogen and Vienna Canyon Diablo Troilite (VCDT) for sulphur. CO_2 and N_2 were used as working standards and were calibrated against primary standards. $\delta^{34}S$ ratios were calculated against a calibration curve using primary standards. Reference gases (CO_2, N_2, SO_2) were checked on a regular basis. Analytical precision was in the range of ±0.08‰ for ^{13}C and ^{15}N, and ±0.13‰ for ^{34}S (Hansen et al. 2009).

2.3 Condition analysis

The relative condition factor (K_n) of cod individuals was calculated using the equation (Le Cren 1951)

(2) $K_n = W / a \times TL^b$

where *W* is the gutted weight in g, *TL* the total length in cm, the constant *a* the initial growth index (intercept of the regression line of $\log_{10}W$ versus $\log_{10}TL$ with the y-axis) and *b* the growth coefficient (slope of the regression line).

2.4 Lipid correction

Lipids are depleted in $\delta^{13}C$ and, thus have the potential to severely affect measured $\delta^{13}C$ ratios and hamper comparisons between species with different fat content (Post et al. 2007). Post et al. (2007) highlighted the importance of lipid correction on $\delta^{13}C$ ratios if the lipid content exceeds 5% of the biomass or if the C:N ratio is larger than 3.5. For our data set, all samples showed a C:N ratio larger than 3.5. Therefore, all $\delta^{13}C$ ratios were corrected based on Post et al. (2007), using the formula

(3) $\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$

where $\delta^{13}C_{normalised}$ is an estimate of $\delta^{13}C$ that is normalised for the effects of lipid concentration on $\delta^{13}C$ (Post et al. 2007).

2.5 Statistical analysis

To obtain an overview of the trophic dynamics of Baltic cod, including important prey species, competitors and food web components, isotopic biplots ($\delta^{15}N$ vs. $\delta^{13}C$ and $\delta^{15}N$ vs. $\delta^{34}S$) of all species were created for each SD. To complete the C and N framework data set, data points for relevant additional species sampled in 2014 were added from Mohm (2014): fourbeard rockling (*Enchelyopus cimbrius*) and coalfish (*Pollachius virens*). Furthermore, data points of mesozooplankton groups sampled in 2003/2004 were added for C and N from Agurto (2007): copepods (*Acartia sp.*, *Centropages hamatus*, *Pseudocalanus acuspes* and *Temora longicornis*) and cladocerans (*Evadne nordmanni* and *Podon sp.*). For C, N and S, *Saduria entomon* samples from 2015 were added.

ANCOVA and ANOVA general linear models (GLM) were used to assess differences in C, N or S between SDs and species, as well as to detect ontogenetic diet shifts based on statistical analyses evaluating the relationship of C, N or S vs. TL. An overview of all statistical models run is shown in Appendix 2.1. Statistical analyses were run for 92 of a total of 96 sampled cod. 4 individuals were excluded: 1 cod from SD22 due to the low sample size (n=1), 2 cod from SD24 and 1 cod from SD25 because stable isotope ratios did not lie in a realistic range ($\delta^{15}N < 11.0‰$; $\delta^{34}S < 8.0‰$). Condition analyses were run for 91 cod, as 1 juvenile cod was excluded because no information on gutted weight was available for the calculation of K_n. Furthermore, 1 outlier of flounder was excluded because $\delta^{34}S < 6.0‰$.

To assess the potential for competition between (4) cod and whiting in SD24 and SD25; (5) herring, sprat and three-spined stickleback in SD25; and (6) dab, flounder and plaice in SD22, standard ellipse areas for small samples sizes (SEAc) were calculated for $\delta^{15}N$ vs. $\delta^{13}C$ and $\delta^{15}N$ vs. $\delta^{34}S$. The standard ellipse is to bivariate data as the standard deviation (sd) to univariate data (Batschelet 1981). It describes some data *x* ($\delta^{13}C$ or $\delta^{34}S$) and *y* ($\delta^{15}N$) by its associated covariance matrix (joint variability of *x* and *y*), defining its size and shape, and the means of *x* and *y*, which define its location. Furthermore, the percentage of ellipses overlap was calculated for the proportion of two species *a* and *b* that overlap with each other, the proportion of *a* that overlaps with b, and the proportion of *b* that overlaps with *a*.

Calculations for lipid correction and condition factors, and graphical illustration of isotopic bi-plots were done in Microsoft Excel 2010 (Microsoft Corporation; Redmond, USA). Statistical analyses and isotopic scatterplots were done in MINITAB (Minitab Incorporated; State College, USA, version 14). Standard ellipse areas were calculated within the SIAR (Stable Isotope Analysis in R) package (SIAR, version 4.2)

All statistical results were considered as significant when $p<0.05$

3. RESULTS

(1) Overall trophic structure of the whole community

Figure 7 provides a first overview of the entire data set (i.e., samples for each species lumped without accounting for spatial structure) for $\delta^{15}N$ (as measure of trophic level) and $\delta^{13}C$ (as measure of different diet sources) ratios. The fish community spanned an overall range of 9.6‰ in $\delta^{15}N$, roughly equivalent to 3 trophic levels. Within this community, highest $\delta^{15}N$ ratios and thus, trophic levels, were displayed by fourbeard rockling ($\delta^{15}N$: 14.4±0.4‰), cod ($\delta^{15}N$: 13.3±0.9‰) and whiting ($\delta^{15}N$: 13.7±0.9‰), all of which were characterised by intermediate $\delta^{13}C$ ratios (fourbeard rockling: $\delta^{13}C$: -21.3±0.9‰; cod: $\delta^{13}C$: -20.5±0.5‰; whiting: $\delta^{13}C$: -20.7±0.7‰). The flatfishes American plaice (*Hippoglossoides platessoides*) ($\delta^{15}N$: 13.8‰) and dab ($\delta^{15}N$: 12.8±0.5‰), as well as the spotted dragonet (*Callionymus maculatus*) ($\delta^{15}N$: 13.0‰) displayed $\delta^{15}N$ ratios similar to cod and whiting, with lower $\delta^{13}C$ ratios (American plaice: $\delta^{13}C$: -20.0‰, dab: $\delta^{13}C$: -19.9±0.5‰, spotted dragonet: $\delta^{13}C$: -19.8‰), indicating a more benthic diet. The flatfish flounder ($\delta^{13}C$: -20.1±1.7‰; $\delta^{15}N$: 12.5±1.7‰) was characterised by the larger variance and range in both $\delta^{15}N$ and $\delta^{13}C$ stable isotope ratios ($\delta^{13}C$: from -23.6 to -12.5‰; $\delta^{15}N$: from 9.8 to 17.4‰), indicating a mixed diet and different diet sources among individuals. The flatfishes plaice ($\delta^{15}N$: 11.9±0.7‰) and turbot (*Scophthalmus maximus*) ($\delta^{15}N$: 11.2‰), as well as the lumpfish (*Cyclopterus lumpus*) ($\delta^{15}N$: 11.6±0.8‰) showed lower $\delta^{15}N$ ratios, but similar $\delta^{13}C$ ratios (plaice: $\delta^{13}C$: -19.2±0.9‰, turbot: $\delta^{13}C$: -20.0‰, lumpfish: $\delta^{13}C$: -19.0±0.5‰). The pelagic fish species herring ($\delta^{15}N$: 11.8±1.2‰), sprat ($\delta^{15}N$: 10.5±1.2‰) and the three-spined stickleback ($\delta^{15}N$: 10.0±0.3‰) displayed the lowest $\delta^{15}N$ ratios in the fish community with lower $\delta^{13}C$ than cod and whiting (herring: $\delta^{13}C$: -21.3±0.8‰, sprat: $\delta^{13}C$: -21.8±0.5‰, three-spined stickleback: $\delta^{13}C$: -21.8±0.2‰) indicating a pelagic diet. The benthic isopod *Saduria entomon* ($\delta^{13}C$: -20.8±0.5‰; $\delta^{15}N$: 11.7±0.7‰) showed similar $\delta^{15}N$ and $\delta^{13}C$ ratios to coalfish ($\delta^{13}C$: -20.7±0.5‰; $\delta^{15}N$: 11.8±0.5‰) and smelt ($\delta^{13}C$: -20.7±0.0‰; $\delta^{15}N$: 11.5±0.0‰). The bivalve ocean quahog (*Arctica islandica*) ($\delta^{13}C$: -18.7±0.3‰; $\delta^{15}N$: 9.9±0.2‰) showed higher $\delta^{15}N$ and $\delta^{13}C$ ratios than the blue mussel (*Mytilus edulis*) ($\delta^{13}C$: -20.5±0.5‰; $\delta^{15}N$: 7.2±0.6‰). Isotopic ratios of copepods ($\delta^{13}C$: -24.3±1.3‰; $\delta^{15}N$: 6.1±1.3‰) and cladocerans ($\delta^{13}C$: -24.7±1.6‰; $\delta^{15}N$: 5.4±1.2‰) showed very low $\delta^{15}N$ and $\delta^{13}C$ ratios, indicating pelagic feeding on a very low trophic level. On the other side, the benthic scavengers, common starfish (*Asterias rubens*) ($\delta^{15}N$: 10.4±1.2‰) and red whelk (*Neptunea antiqua*) ($\delta^{15}N$: 11.4±0.7‰) displayed $\delta^{15}N$ ratios similar to the pelagic fish species and flatfishes with lower

$\delta^{15}N$ ratios. Based on their $\delta^{13}C$ ratios (common starfish: $\delta^{13}C$: -18.2±0.5‰, red whelk: $\delta^{13}C$: -17.3±0.4‰) both benthic scavengers showed low values indicating a benthic diet.

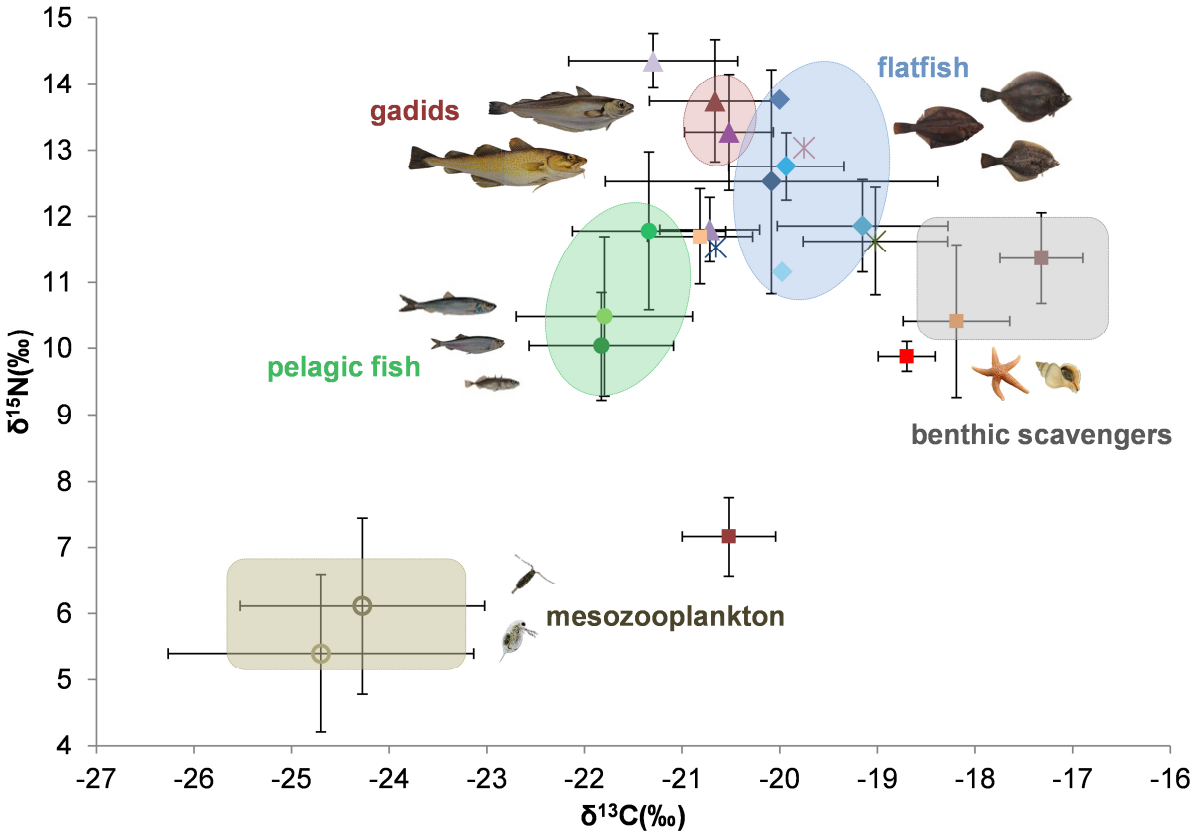

Figure 7. Biplot of mean $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) of all sampled individuals per species (not accounting for spatial structure); standard deviation is represented by error bars; coloured ovales highlight our three specific study groups: (red) gadids: ▲cod, ▲whiting; (blue) flatfish: ◆dab, ◆flounder, ◆plaice; (green) pelagic fish: ●herring, ●sprat, ●three-spined stickleback; coloured rectangles highlight (brown) mesozooplankton: ○cladocerans, ○copepods (Agurto 2007); (grey) benthic scavengers: ■common starfish, ■red whelk (April 2016); non-highlighted species (April 2016) flatfish: ◆American plaice, ◆turbot; filter feeders: ■blue mussel, ■ocean quahog; cyclopertids: ✶lumpfish; osermids: ✶smelt, callionymids: ✶spotted dragonet; (August 2015) benthic scavenger: ■*Saduria entomon*; (April 2014) gadids: ▲coalfish, ▲fourbeard rockling. Fish illustrations from Muus et al. (1999), photographs: copepod by Peter J. Bryant, cladoceran by Hans-Otto Siebeck, common starfish by Hans Hillewaert, red whelk by Guido and Philippe Poppe.

To specifically assess benthic versus pelagic feeding, for which S is an ideal indicator, figure 8 presents an overview of the $\delta^{15}N$ (as measure of trophic level) and $\delta^{34}S$ (as measure of benthic versus pelagic feeding) ratios of all sampled individuals per species (not accounting for spatial structure). Flatfishes American plaice ($\delta^{34}S$: 11.9‰), dab ($\delta^{34}S$: 12.6±1.7‰), flounder ($\delta^{34}S$: 11.8±2.3‰) and plaice ($\delta^{34}S$: 12.7±1.8‰), as well as the spotted dragonet ($\delta^{34}S$:11.5‰) and *Saduria entomon* ($\delta^{34}S$:12.4±2.0‰) showed low $\delta^{34}S$ ratios, indicating a benthic diet. Most interestingly, flatfishes, in particular flounder ($\delta^{34}S$: from 4.7 to 14.8‰), and *Saduria entomon* ($\delta^{34}S$: from 9.9 to 15.4‰) showed a very large variance in $\delta^{34}S$ ratios,

suggesting the presence of ecological niches. In contrast, high $\delta^{34}S$ ratios were represented by the pelagic fish species herring ($\delta^{34}S$: 15.6±0.8‰), sprat ($\delta^{34}S$: 16.5±0.8‰) and the three-spined stickleback ($\delta^{34}S$: 18.4±0.3‰), together with lumpfish ($\delta^{34}S$: 16.3±0.7‰) and turbot ($\delta^{34}S$: 16.9‰), indicating a pelagic diet. Cod ($\delta^{34}S$: 14.0±1.5‰) showed intermediate $\delta^{34}S$ ratios, indicating a benthic and pelagic diet, whereas whiting ($\delta^{34}S$: 15.6±1.5‰) displayed higher $\delta^{34}S$ ratios, indicating a more pelagic diet. The benthic invertebrates blue mussel ($\delta^{34}S$: 15.8±0.6‰), common starfish ($\delta^{34}S$: 15.6±1.6‰), ocean quahog ($\delta^{34}S$: 14.4±0.4‰) and red whelk ($\delta^{34}S$: 15.3±0.9‰) showed similar $\delta^{34}S$ ratios to cod and whiting, indicating benthic and pelagic prey sources.

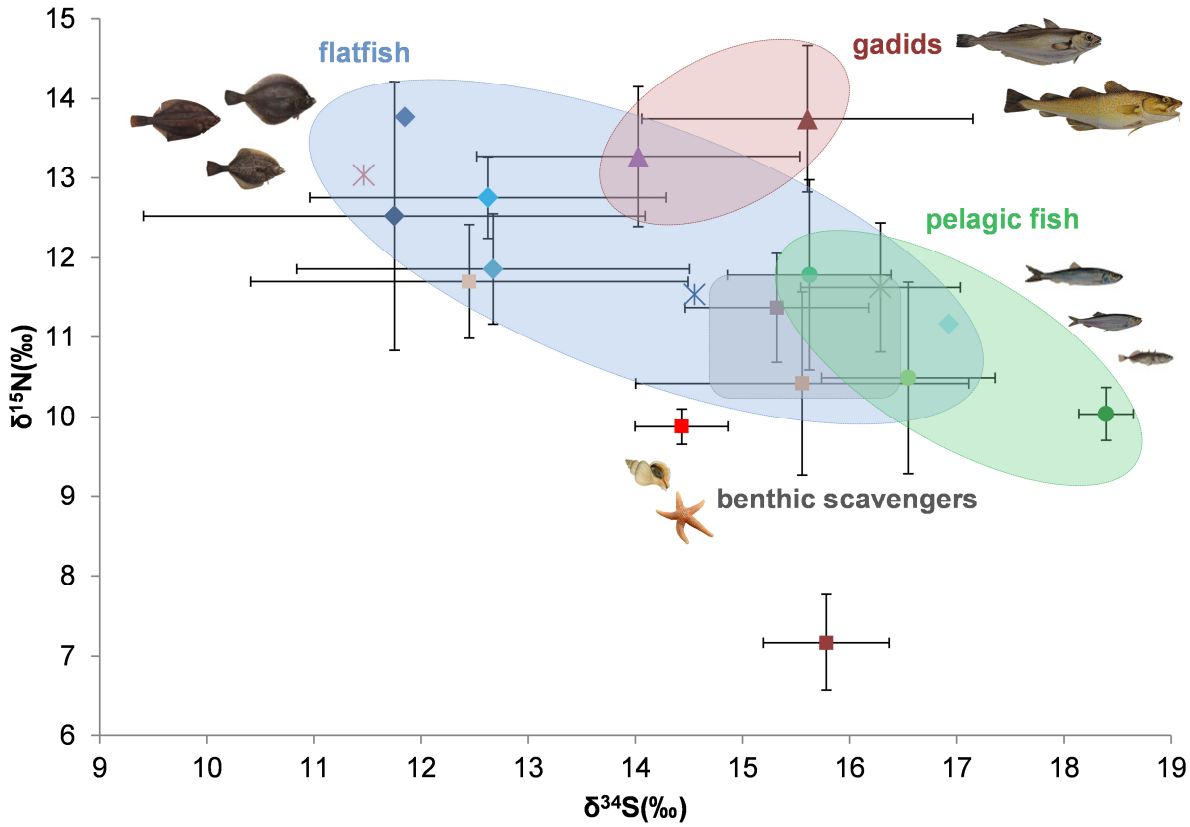

Figure 8. Biplot of mean $\delta^{15}N$ (‰) and $\delta^{34}S$ (‰) of all sampled individuals per species (not accounting for spatial structure); standard deviation is represented by error bars; coloured ovales highlight our three specific study groups: (red) gadids: ▲cod, ▲whiting; (blue) flatfish: ◆dab, ◆flounder, ◆plaice; (green) pelagic fish: ●herring, ●sprat, ●three-spined stickleback; coloured rectangle highlights (grey) benthic scavengers: ■common starfish, ■red whelk (April 2016); non-highlighted species (April 2016) flatfish: ◆American plaice, ◆turbot; filter feeders: ■blue mussel, ■ocean quahog; cyclopertids: ✳lumpfish; osermids: ✳smelt, callionymids: ✳spotted dragonet; (August 2015) benthic scavenger: ■*Saduria entomon*. Fish illustrations from Muus et al. (1999), photographs: copepod by Peter J. Bryant, cladoceran by Hans-Otto Siebeck, common starfish by Hans Hillewaert, red whelk by Guido and Philippe Poppe.

An overview of SIA results of all 296 samples is shown in Appendix 2.2.

(2) Ontogenetic diet shifts and spatial differences in cod

Cod showed a significant shift to higher $\delta^{34}S$ ratios with increasing body size (ANCOVA GLM: F=33.31, p<0.001) (Figure 9; Table 2), consistent with a shift from benthic to pelagic prey. In contrast, no significant ontogenetic diet shift was detected in $\delta^{13}C$ ratios (Figure 10; Table 3) or $\delta^{15}N$ (Figure 11; Table 4). Spatial differences between SD were significant for S (ANCOVA GLM: F=3.49, p=0.035) (Table 2), but not C (Table 3) or N (Table 4). The overall variability explained by the GLMs was 29.94% for S, 2.18% for C, and 24.58% for N.

Table 2. Summary of results of ANCOVA general linear model (GLM) of cod (n=92), with $\delta^{34}S$ as response variable, SD and SD*TL as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=29.94%. SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
SD	2	1.1913	7.265	3.633	3.49	0.035
TL	1	30.430	34.682	34.682	33.31	0.000
SD*TL	2	5.914	5.914	2.957	2.84	0.064
Error	86	89.544	89.544	1.041		
Total	91	127.801				

Table 3. Summary of results of ANCOVA general linear model (GLM) of cod (n=92), with $\delta^{13}C$ as response variable, SD and SD*TL as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=2.18%. SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
SD	2	0.3652	0.1339	0.0670	0.30	0.743
TL	1	0.0144	0.0269	0.0269	0.12	0.731
SD*TL	2	0.0521	0.0521	0.0261	0.12	0.891
Error	86	19.3555	19.3555	0.2251		
Total	91	19.7873				

Table 4. Summary of results of ANCOVA general linear model (GLM) of cod (n=92), with $\delta^{15}N$ as response variable, SD and SD*TL as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=24.58%. SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
SD	2	10.2124	2.2502	1.1251	2.81	0.066
TL	1	0.0704	0.4886	0.4886	1.22	0.272
SD*TL	2	0.9263	0.9263	0.4631	1.16	0.319
Error	86	34.3940	34.3940	0.3999		
Total	91	45.6031				

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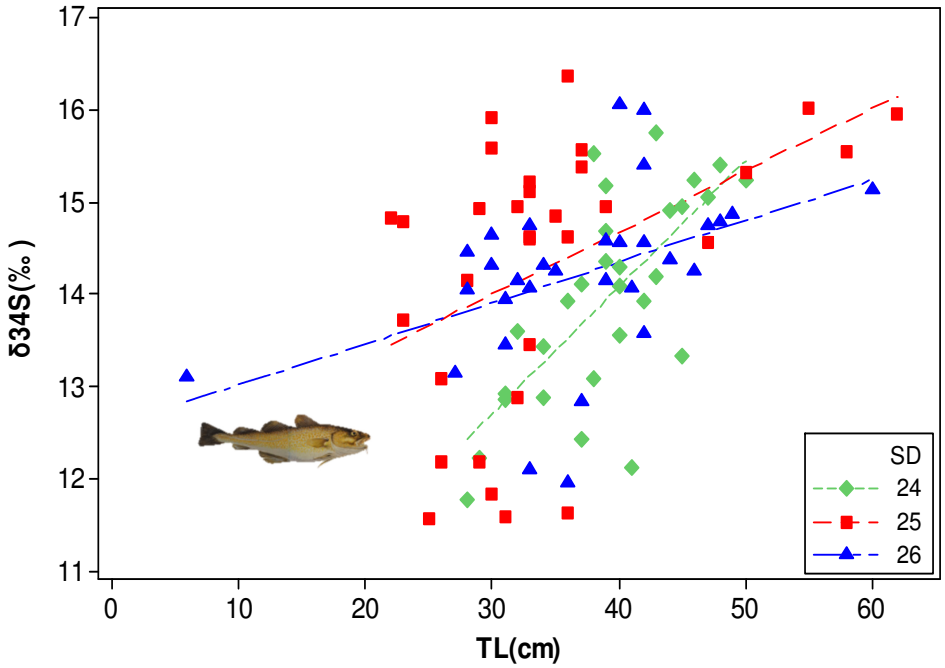

Figure 9. Scatterplot of $\delta^{34}S$ (‰) and TL (cm) for cod per SD; dotted lines represent regression lines; ◆ SD24 – Arkonas Basin, ■ SD25 – Bornholm Basin, ▲ SD26 – Gdansk Deep. Fish illustration from Muus et al. (1999).

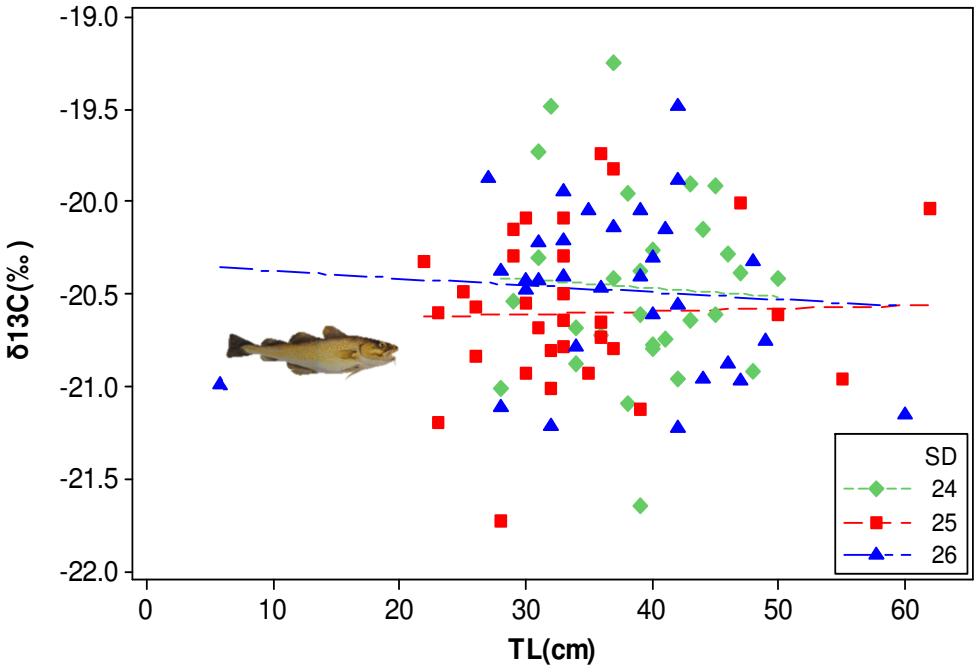

Figure 10. Scatterplot of $\delta^{13}C$ (‰) and TL (cm) for cod per SD; dotted lines represent regression lines; ◆ SD24 - Arkona Basin, ■ SD25 - Bornholm Basin, ▲ SD26 - Gdansk Deep. Fish illustration from Muus et al. (1999).

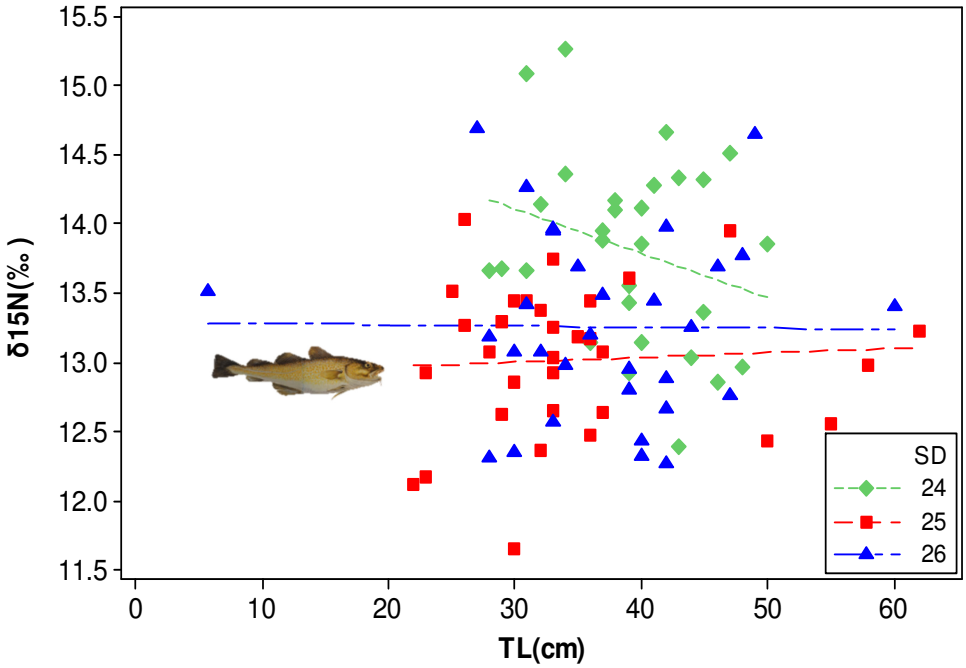

Figure 11. Scatterplot of $\delta^{15}N$ (‰) and TL (cm) for cod per SD; dotted lines represent regression lines; ◆ SD24 – Arkona Basin, ■ SD25 – Bornholm Basin, ▲ SD26 – Gdansk Deep. Fish illustration from Muus et al. (1999).

The following section will focus on patterns related to benthic versus pelagic feeding, and therefore display only $\delta^{34}S$ results. Additional graphs for $\delta^{13}C$ and $\delta^{15}N$ can be found attached in the Appendix.

(3) Body condition of cod in relation to the benthos proportion in the diet (as indicated by sulphur stable isotope ratios)

No significant correlation was found between K_n and $\delta^{34}S$ (ANCOVA GLM: F=2.67, p=0.106) (Figure 12; Table 5), i.e., there was no change in the relative condition factor ($\delta^{34}S$) with increasing benthos proportion in the diet (as indicated by decreasing $\delta^{34}S$ ratios). Therefore, the null hypothesis could not be rejected. However, a positive trend of K_n with an increase in consumed benthos (a decrease in $\delta^{34}S$) was visible in all three basins. Furthermore, there were no significant differences found between SD (Table 5). The model explained an overall variability of 17.98%.

Table 5. Summary of results of ANCOVA general linear model (GLM) of cod (n=91), with K_n (relative condition factor) as response variable, SD and SD*$\delta^{34}S$ as explanatory variables, and $\delta^{34}S$ as covariate. Overall variability explained by the model was R^2=17.98%. SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
SD	2	0.23399	0.00077	0.00038	0.02	0.976
$\delta^{34}S$	1	0.05395	0.04191	0.04191	2.67	0.106
SD*$\delta^{34}S$	2	0.00421	0.00421	0.00211	0.13	0.874
Error	85	1.33289	1.33289	0.01568		
Total	90	1.62504				

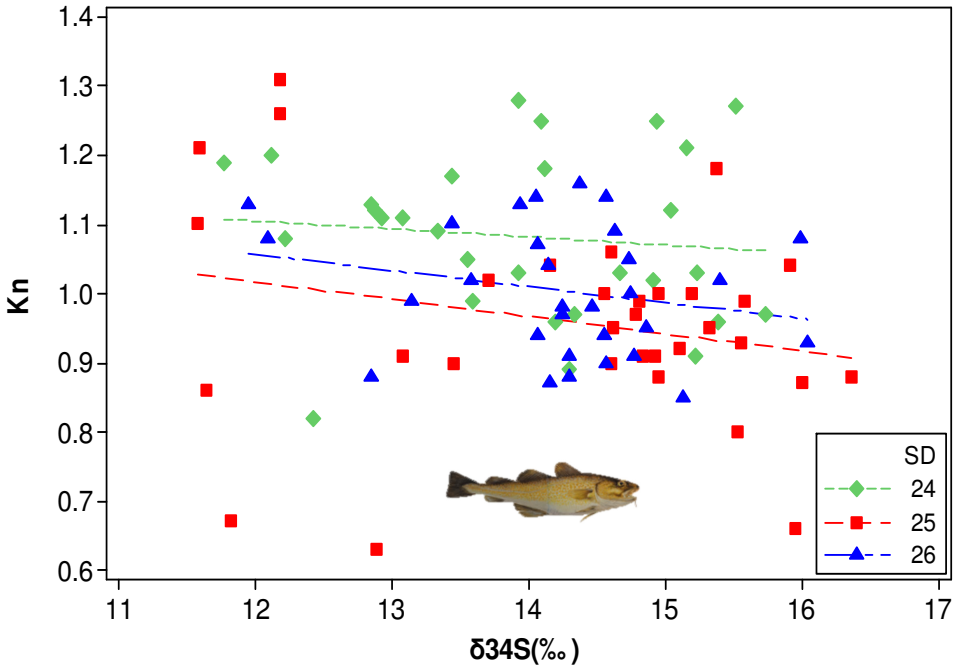

Figure 12. Scatterplot of K_n and $\delta^{34}S$ (‰) for cod per SD; dotted lines represent regression lines; ◆ SD24 – Arkona Basin, ■ SD25 – Bornholm Basin, ▲ SD26 – Gdansk Deep. Fish illustration from Muus et al. (1999).

(4) Interspecific competition between cod and whiting

For both SD24 and 25, $\delta^{34}S$ ratios of cod and whiting were significantly correlated with TL (ANCOVA GLM: F=28.24, p<0.001) (Figure 13,14; Table 6). Furthermore, differences between SD (ANCOVA GLM: F=8.88, p=0.004) and species (ANCOVA GLM: F=57.81, p<0.001) were significant (Table 6). An overall variability of 48.0% was explained by the model. In contrast, no significant correlation of TL with, nor differences between SD or species were found for $\delta^{13}C$ (Appendix 2.3). For $\delta^{15}N$, only differences between SD were found to be significant (Appendix 2.4).

The significant species differences and ontogenetic diet shifts to higher $\delta^{34}S$ ratios are clearly visible in both SD24 (Figure 13) and SD25 (Figure 14).

Table 6. Summary of results of ANCOVA general linear model (GLM) of cod (n=61) and whiting (n=17), with $\delta^{34}S$ as response variable, SD, species and SD*species as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=48.0%. SD24 – Arkona Basin, SD25 – Bornholm Basin.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	7.235	33.997	33.997	28.24	<0.001
SD	1	4.285	10.686	10.686	8.88	0.004
Species	1	69.229	69.591	65.591	57.81	<0.001
SD*species	1	0.384	0.384	0.384	0.32	0.574
Error	73	87.877	87.877	1.204		
Total	77	169.010				

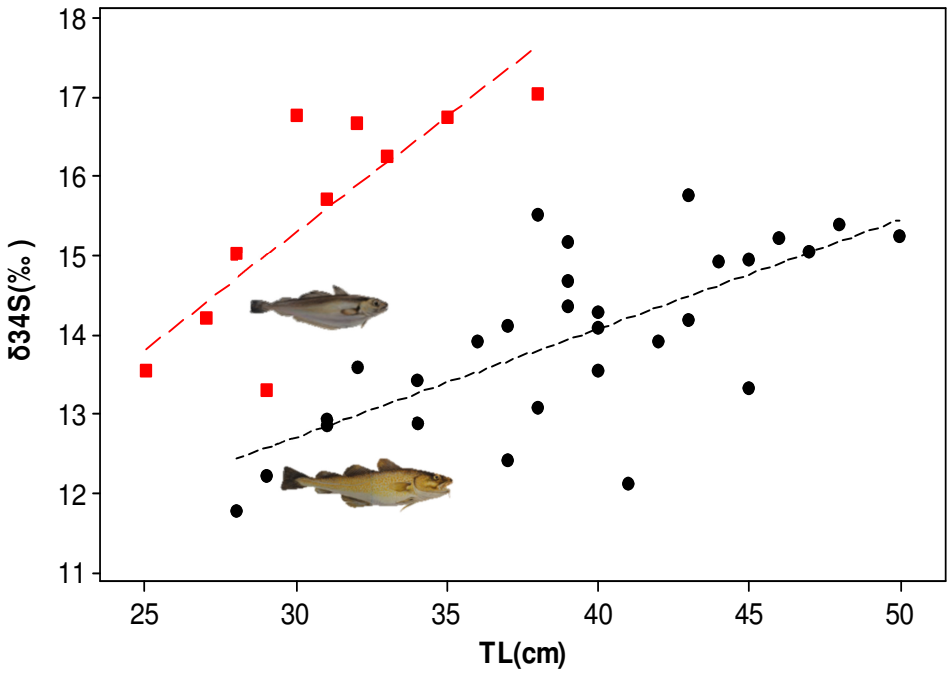

Figure 13. Scatterplot of $\delta^{34}S$ (‰) and TL (cm) for cod and whiting of SD24 – Arkona Basin; dotted lines represent regression lines; ● cod, ■ whiting. Fish illustrations from Muus et al. (1999).

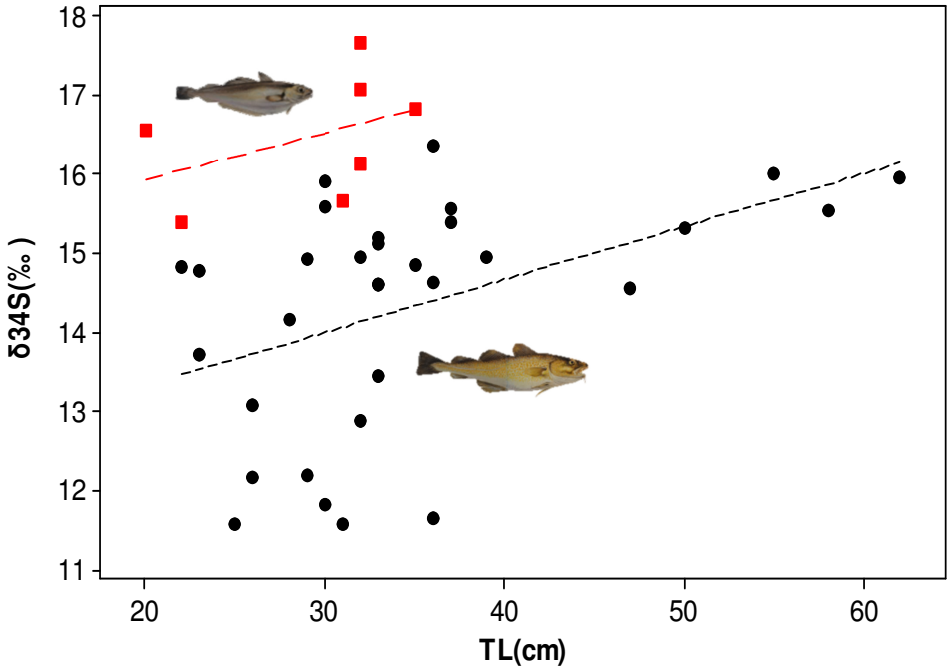

Figure 14. Scatterplot of $\delta^{34}S$ (‰) and TL (cm) for cod and whiting of SD25 – Bornholm Basin; dotted lines represent regression lines; ● cod, ■ whiting. Fish illustrations from Muus et al. (1999).

The overlap in $\delta^{15}N$ vs. $\delta^{34}S$ niche space between cod and whiting is shown in Figures 15 for SD24 and 16 for SD25. In SD24, the two species shared an overlap of 10.86% for, whereby cod overlapped 16.85% with whiting (cod/whiting), and whiting 65.05% with cod (whiting/cod) (Figure 15). For SD25, cod and whiting overlapped 0.14%, cod/whiting 0.22%, and whiting/cod 0.42% (Figure 16). The only partial niche overlap in both basins was explained by lower $\delta^{34}S$ ratios in cod compared to whiting. In both SD24 and SD25, the SEAc of cod, and thus its isotopic niche, was larger than the SEAc of whiting. Overlap in $\delta^{15}N$ vs. $\delta^{13}C$ niche space is given in Appendix 1.3 and 1.6.

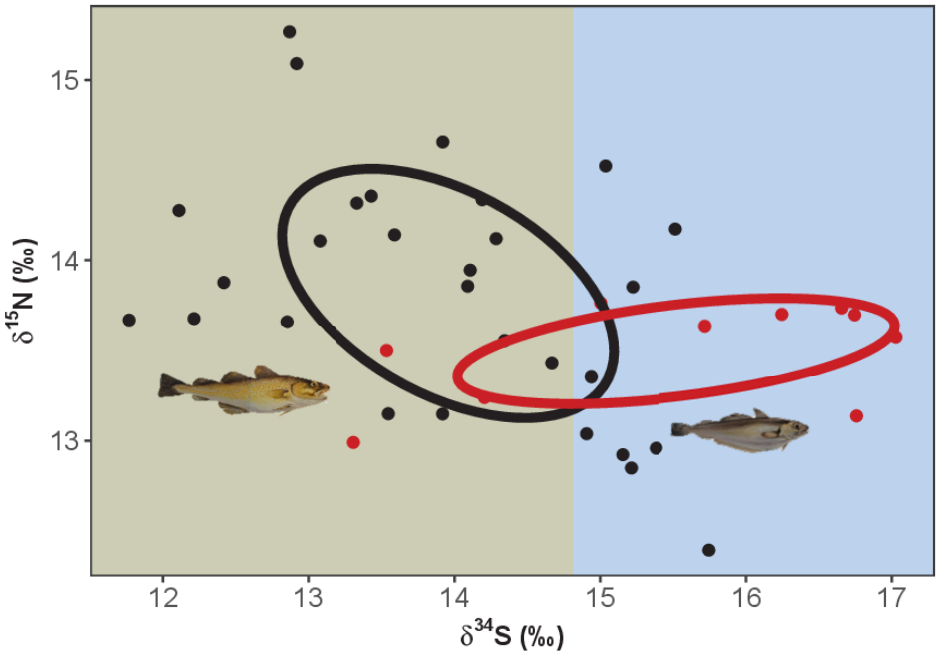

Figure 15. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{34}S$ (‰) between cod and whiting of SD24 – Arkona Basin; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; the brown rectangle represents the $\delta^{34}S$ range of flatfish, the blue rectangle the $\delta^{34}S$ range of clupeids from SD24; ● cod, ● whiting. Fish illustrations from Muus et al. (1999).

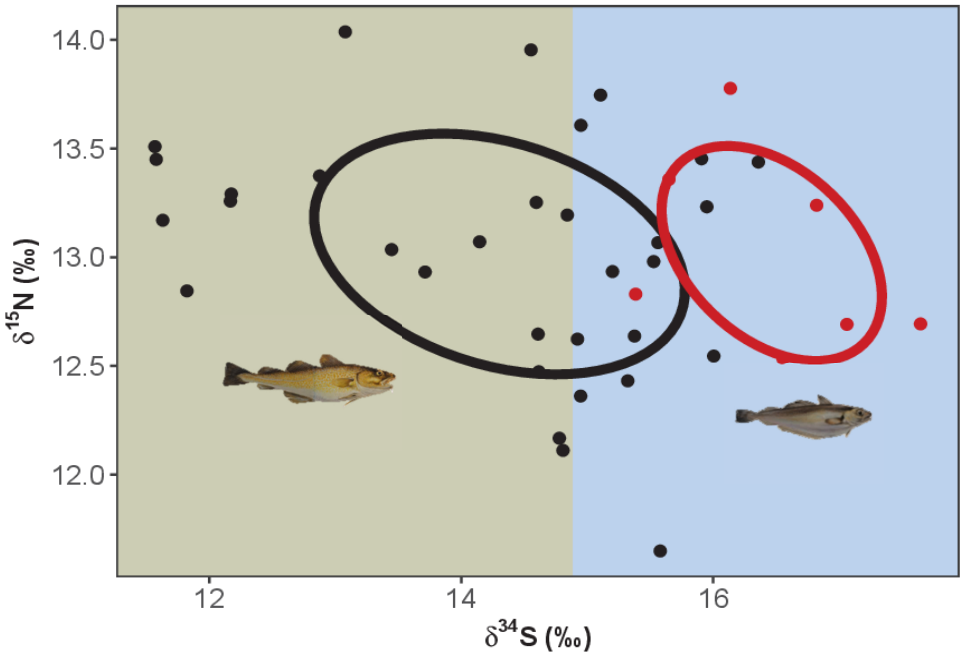

Figure 16. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{34}S$ (‰) between cod and whiting of SD25 – Bornholm Basin; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; the brown rectangle represents the $\delta^{34}S$ range of flatfish, the blue rectangle the $\delta^{34}S$ range of clupeids from SD25; ● cod, ● whiting. Fish illustrations from Muus et al. (1999).

(5) Interspecific competition between herring, sprat and three-spined stickleback

For SD25, statistical analyses of herring, sprat and three-spined stickleback revealed significant differences between species for $\delta^{34}S$ (ANOVA GLM: F=56.57, p<0.001) (Figure 17; Table 7) and for $\delta^{15}N$ (Appendix 2.5). The overall variability explained by the models was 81.32% for S, and 59.63% for N. In contrast, no significant differences between species were found for $\delta^{13}C$ (Appendix 2.6).

Table 7. Summary of results of ANOVA general linear model (GLM) of herring (n=10), sprat (n=10) and three-spined stickleback (n=9), with $\delta^{34}S$ as response variable, and species as explanatory variables. Overall variability explained by the model was R^2=81.32%. SD25 – Bornholm Basin.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Species	2	28.428	28.428	14.214	56.57	<0.001
Error	26	6.532	6.532	0.251		
Total	28	34.961				

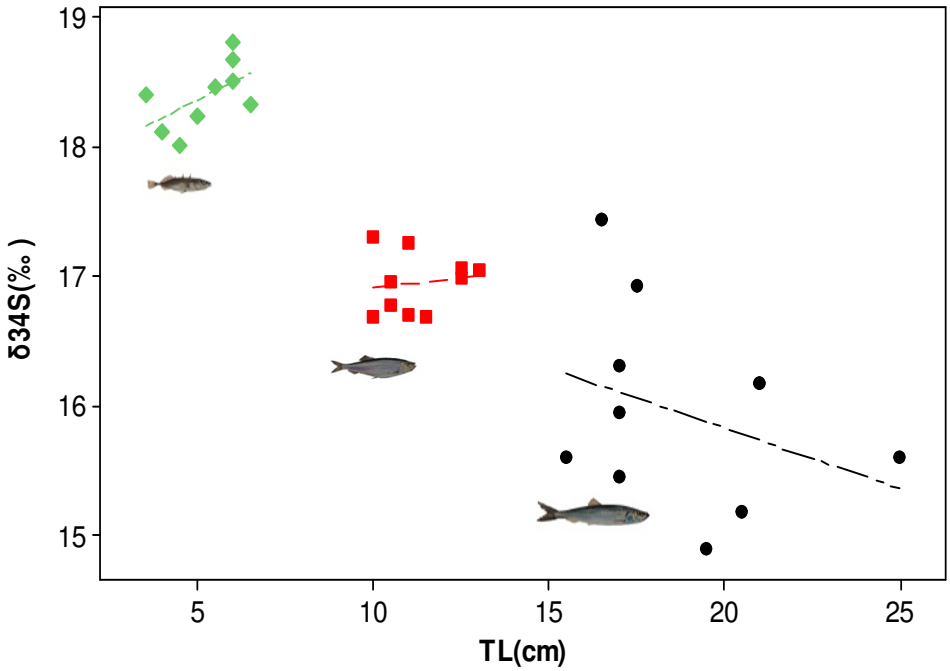

Figure 17. Scatterplot of $\delta^{34}S$ (‰) and TL (cm) for herring, sprat and three-spined stickleback of SD25 – Bornholm Basin; dotted lines represent regression lines; ● herring, ■ sprat, ◆ three-spined stickleback. Fish illustrations from Muus et al. (1999).

Figure 18 shows the $\delta^{15}N$ vs. $\delta^{34}S$ niche spaces of herring, sprat and the three-spined stickleback for SD25. No isotopic niche overlap was found for any of the species. Herring displayed the largest SEAc within the pelagic fish community. Overlap in $\delta^{15}N$ vs. $\delta^{13}C$ niche space is given in Appendix 1.9.

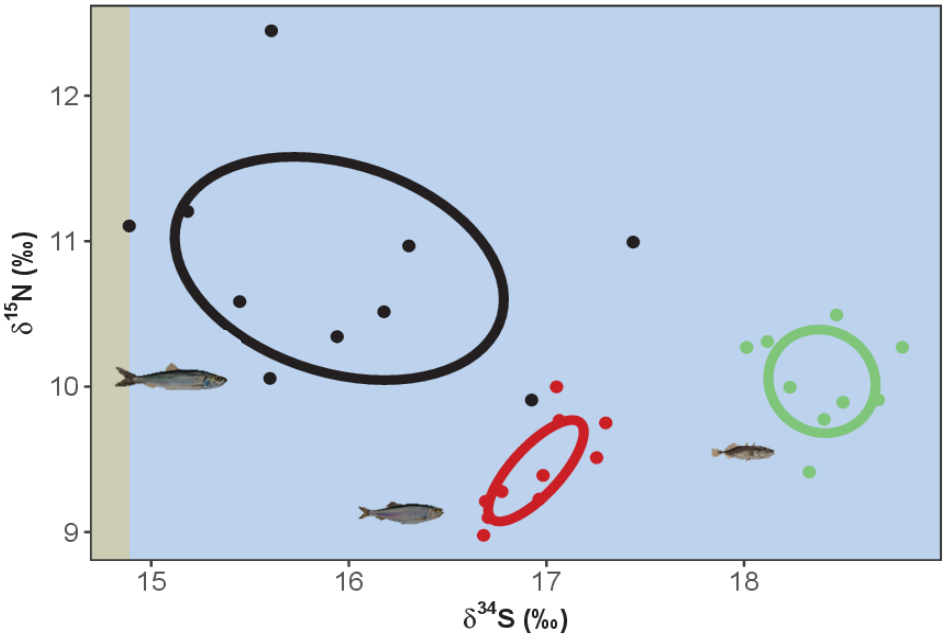

Figure 18. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{34}S$ (‰) between herring, sprat and three-spined stickleback of SD25 – Bornholm Basin; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; the brown rectangle represents the $\delta^{34}S$ range of flatfish, the blue rectangle the $\delta^{34}S$ range of clupeids from SD25; ● herring, ● sprat, ● three-spined stickleback. Fish illustrations from Muus et al. (1999).

(6) Interspecific competition between dab, flounder and plaice

For SD22, statistical analyses revealed significant differences between species for $\delta^{34}S$ (ANCOVA GLM: F=8.31, p=0.002) (Figure 19; Table 8) and for $\delta^{13}C$ (Appendix 2.7). The overall variability explained by the models was 62.57% for S, and 55.42% for C. In contrast, no significant differences between species were found for $\delta^{15}N$ (Appendix 2.8).

Table 8. Summary of results of ANCOVA general linear model (GLM) of dab (n=10), flounder (n=9) and plaice (n=7), with $\delta^{34}S$ as response variable, species and species*TL as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=62.57%. SD22 – Kiel Bight.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	30.522	5.435	5.5435	2.62	0.121
species	2	6.880	34.503	17.251	8.31	0.002
species*TL	2	21.957	31.597	15.987	7.70	0.003
Error	20	41.500	41.500	2.075		
Total	25	110.877				

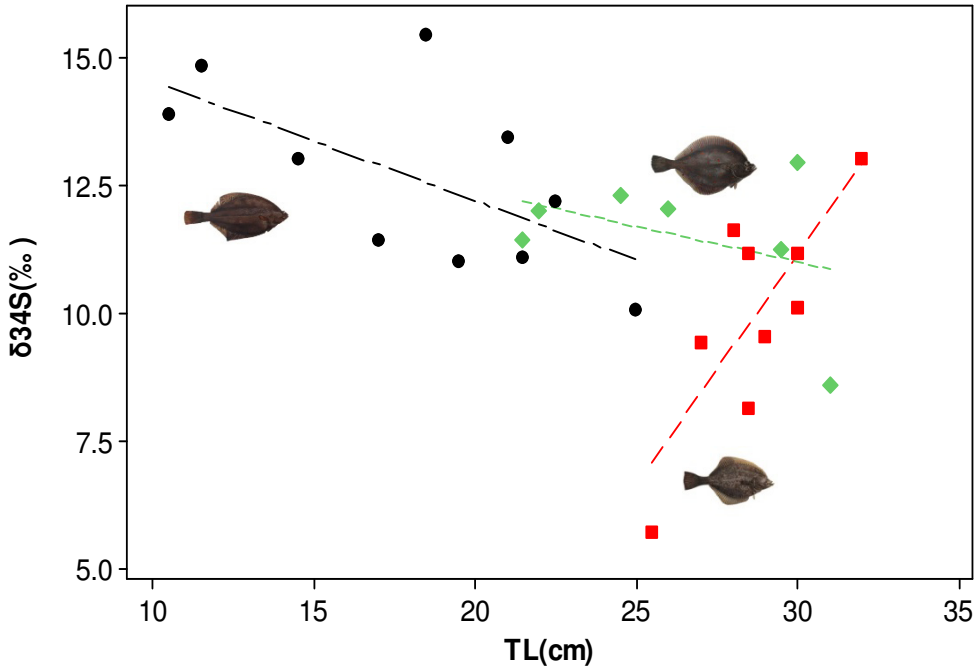

Figure 19. Scatterplot of $\delta^{34}S$ (‰) and TL (cm) for dab, flounder and plaice of SD22 – Kiel Bight; dotted lines represent regression lines; ● dab, ■ flounder, ◆ plaice. Fish illustrations from Muus et al. (1999).

The overlap in $\delta^{15}N$ vs. $\delta^{34}S$ niche space between dab, flounder and plaice for SD22 is shown in Figure 20. Dab and flounder shared an overlap of 5.98%, dab/flounder 18.35%, and flounder/dab 8.87%. Dab and plaice overlapped 17.07%, dab/plaice 32.44%, and plaice/dab 36.06%. Furthermore, flounder and plaice displayed an overlap of 22.63%, flounder/plaice

32.48%, and plaice/flounder 74.59%. The largest SEAc was displayed by flounder. Overlap in $\delta^{15}N$ vs. $\delta^{13}C$ niche space is given in Appendix 1.12.

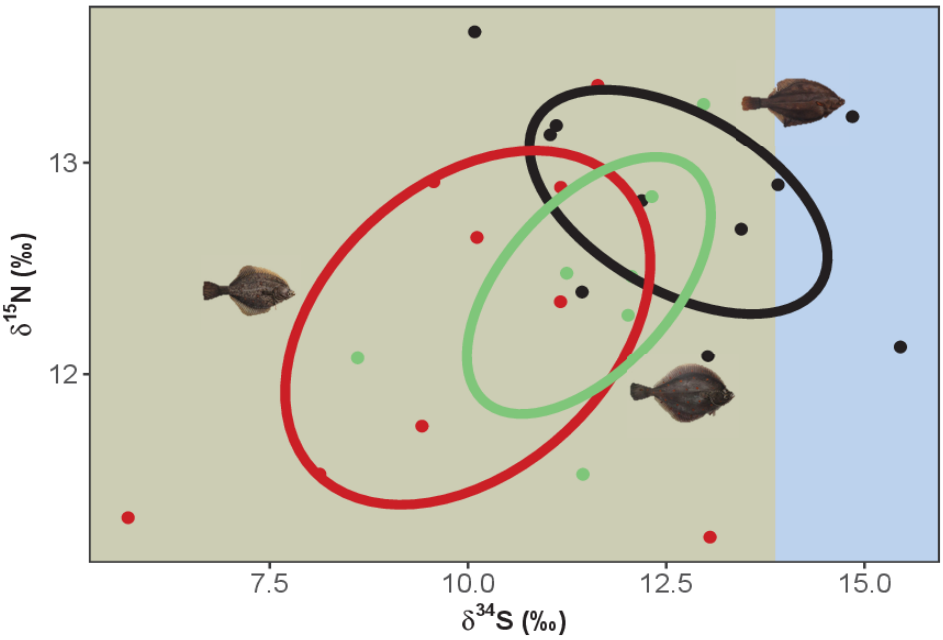

Figure 20. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{34}S$ (‰) between dab, flounder and plaice of SD22 – Kiel Bight; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines the brown rectangle represents the $\delta^{34}S$ range of flatfish, the blue rectangle the $\delta^{34}S$ range of clupeids from SD22; ● dab, ● flounder, ● plaice. Fish illustrations from Muus et al. (1999).

4. DISCUSSION

The main objective of this study was to elucidate the trophic dynamics of Baltic fish species after the 2014 MBI event. My data broadly confirms previous findings from feeding ecology studies in the Baltic Sea, but expands the range of species included in the assessment and provides new insights, in particular based on the $\delta^{34}S$ analysis.

(1) Overall trophic structure of the whole community

The overall structure of the fish community was consistent with broad expectations (Table 9), with the group of the larger fish predators cod and whiting displaying the highest, flatfishes intermediate, and the planktivores the lowest trophic level. At the same time, there were some surprising findings, such as the large intrapopulation variability of $\delta^{34}S$ ratios found in flatfishes, in particular flounder, indicating a large isotopic niche space. This finding would be consistent with the existence of different feeding strategies, which may be feeding on a benthic, pelagic, or mixed diet (Mulicki 1947). Another surprising finding was the low $\delta^{15}N$ and high $\delta^{34}S$ signature of turbot within the flatfish community. In fact, maybe unexpected, turbot often leave the bottom to hunt in the pelagic for fishes (Holmes & Gibson 1983), which could explain the rather pelagic $\delta^{34}S$ signature. It is, however difficult to compare the $\delta^{15}N$ signature of turbot with those of other species within the flatfish community due to the fact that $\delta^{15}N$ baselines between benthic and pelagic food webs appear to differ, i.e. if turbot feeds pelagic as indicated by high $\delta^{34}S$ ratios, and e.g. plaice feeds benthic as indicated by low $\delta^{34}S$ ratios, their $\delta^{15}N$ may not be directly comparable. This is particularly important for general conclusions that are made on results only based on N (Bowes et al. 2017). Therefore, conclusions on the feeding ecology of Baltic species are here drawn in the light of both N and S signatures, and broadly corroborate previous findings from SCA studies.

An overview of the SIA results of all species included in the isotopic biplots, and their diet preferences based on the presented SIA results in comparison to conclusions from previous studies can be found in Table 9.

Table 9. Overview of SIA results of all species included in the isotopic biplots, and their diet preferences based on conclusions from the here in presented SIA results, shown in comparison to conclusions from previous studies. $\delta^{15}N$ and $\delta^{34}S$ ($\delta^{13}C$) ratios are divided into groups (high, low, intermediate) and subgroups (intermediate-low, intermediate-high) to better identify their position in the food web.

Species	$\delta^{15}N$	$\delta^{34}S$ ($\delta^{13}C$)	SIA conclusion	Literature conclusion	References
Cod	high	intermediate	fish predator, pelagic and benthic diet	pelagic fish, benthos	(Bagge et al. 1994)
Whiting	high	intermediate-high	fish predator, mainly pelagic diet	mainly pelagic fish, benthos	(Ross et al. 2016)
Dab	intermediate	low	mainly benthic diet, invertebrates and fish	benthic invertebrates, fish	(Hoeines & Bergstad 2002)
Flounder	intermediate	low	mainly benthic diet, invertebrates and fish	benthic invertebrates, fish	(Arntz & Finger 1981)
Plaice	intermediate-low	low	benthic invertebrates	mainly benthic invertebrates, fish	(Hoeines & Bergstad 2002)
Herring	intermediate-low	intermediate-high	predominantly pelagic secondary consumer	zooplankton, nektobenthos	(Casini et al. 2004, Möllmann et al. 2004)
Sprat	low	high	pelagic secondary consumer	uooplankton	(Möllmann et al. 2004)
Three-spined stickleback	low	high	pelagic secondary consumer	zooplankton, (nekto)benthos	(Jakubavičiūtė et al. 2017a, 2017b)
Fourbeard rockling	high	(intermediate)	fish predator, benthic and pelagic diet	benthic invertebrates, fish	(Lampart-Kałużnicka & Heese 2015)
American plaice	high	low	fish predator, predominantly benthic diet	benthic invertebrates, fish	(Arntz & Finger 1981)
Spotted dragonet	intermediate	low	mainly benthic diet, invertebrates and fish	benthic invertebrates	(Bauchot 1986)

Species	$\delta^{15}N$	$\delta^{34}S$ ($\delta^{13}C$)	SIA conclusion	Literature conclusion	References
Lumpfish	intermediate-low	high	pelagic secondary consumer	small crustaceans, jellyfish	(Muus et al. 1999)
Smelt	intermediate-low	intermediate	secondary consumer, pelagic and benthic diet	pelagic and benthic invertebrates, fish	(Taal et al. 2013)
Saduria entomon	intermediate-low	low	secondary consumer, benthic invertebrates	benthic invertebrates, scavenger	(Haahtela 1990)
Turbot	intermediate-low	high	pelagic secondary consumer	mainly fish, benthic invertebrates	(Arntz & Finger 1981)
Red whelk	intermediate-low	intermediate	secondary consumer, pelagic and benthic diet	benthic invertebrates, scavenger	(Taylor 1978)
Common starfish	low	intermediate-high	secondary consumer, mainly pelagic diet	benthic invertebrates, scavenger	(Anger et al. 1977)
Ocean quahog	low	intermediate	secondary consumer, pelagic and benthic diet	filter feeder	(Liehr et al. 2005)
Blue mussel	very low	intermediate-high	primary consumer, mainly pelagic diet	filter feeder	(Haamer & Rodhe 2000)
Copepods	very low	(very low)	primary consumer, pelagic diet	phytoplankton	(Agurto 2007)
Cladocerans	very low	(very low)	primary consumer, pelagic diet	phytoplankton	(Agurto 2007)

(2) Ontogenetic diet shifts and spatial differences in cod

To assess the feeding ecology of Baltic cod, in particular ontogenetic diet shifts from benthic to pelagic prey, and spatial differences in feeding patterns, C, N and S were used simultaneously. As C did not appear to be powerful enough to display benthic-pelagic shifts in the Baltic Sea, I will here focus on $\delta^{34}S$ results only.

The found ontogenetic diet shift from benthic (low $\delta^{34}S$ ratios) to pelagic (high $\delta^{34}S$ ratios) feeding with increasing fish size of cod, confirms previous results demonstrating that juvenile cod (TL <20 cm) feed mainly on benthic invertebrates such as small crustaceans (*Mysis sp*., *Pontopoeira sp.*) (Bagge et al. 1994), and then gradually shift to a predominantly piscivore diet, whereby sprat, followed by herring, are preferred prey species (Pachur & Horbowy 2013). The overall large range in $\delta^{34}S$ ratios shown by adult fishes of similar size suggests that they complement their mainly piscivore diet with benthic food resources. This corroborates previous reports showing that adult cod also feed on benthic invertebrates such as *Saduria entomon*, yet the importance of benthic prey items for adults has decreased as a result of dropping oxygen levels (Möllmann et al. 2009, Casini et al. 2016). After the 2014 MBI event, we would expect that the benthos proportion in cod's diet may have increased again which would result in less pelagic (lower $\delta^{34}S$) values for adult fish. However, without temporal comparisons assessing changes in the strength of ontogenetic shifts in cod that could be related to higher benthos consumption by adult fish, this question is difficult to assess. Furthermore, the strength of ontogenetic diet shifts in cod is difficult to detect without sufficient juvenile cod data.

The observed spatial differences in $\delta^{34}S$ ratios confirm the assumption that there is a strong potential for the existence of different baselines between basins (Mohm 2014).

These findings show that ontogenetic diet shifts are present in all basins, but more juvenile cod data is needed, to assess the strength of such shifts. Besides, relating the benthos proportion in the diet of cod with oxygen levels and assumed higher benthos availability requires a high temporal resolution in further studies.

(3) Body condition of cod in relation to the benthos proportion in the diet (as indicated by sulphur stable isotope ratios)

To understand the reasons behind the drastic decline in body condition of cod, I tested whether there is a correlation of the relative condition factor (K_n) with the benthos proportion in the diet (as indicated by $\delta^{34}S$ ratios).

No significant correlation was found, thus the null hypothesis could not be rejected. However, there was a positive trend in all three basins, suggesting that body condition of cod increases with an increasing benthos proportion in the diet (as indicated by decreasing $\delta^{34}S$ ratios). A previous report of the Study Group on Spatial Analysis for the Baltic SEA (SGSPATIAL) demonstrated that there was no relation of body condition or anoxic areas with benthic prey in cod stomachs (ICES 2014). However, all cod, no matter their body condition, showed an overall lower food intake of both pelagic and benthic in areas of hypoxia. This may be caused by a decrease in benthos availability, and a change in feeding behaviour forcing cod to become more pelagic and thus feeding predominantly on herring and sprat (ICES 2014). The findings presented here showed that small cod did have access to benthic prey, yet enough data on juveniles is lacking to assess the strength in ontogenetic diet shifts more clearly.

So far, we know that hypoxic areas play a key role in driving body condition of cod, yet there are several mechanisms, which do not necessarily act independently from each other (Casini et al. 2016).

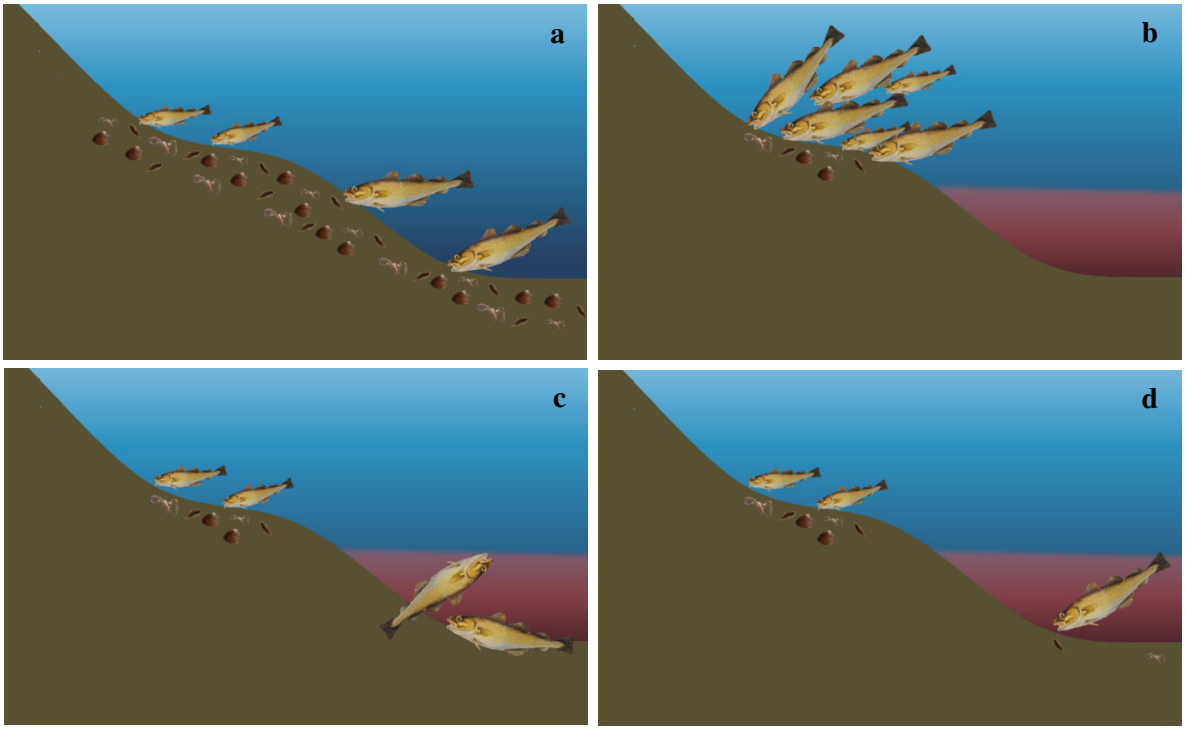

Figure 21. Graphic representation of (a) cod under ideal conditions with benthos being ubiquitously available for both juvenile and adult cod; and of the mechanisms potentially driving cod condition due to the presence of hypoxic areas (red area): (b) habitat compression: high densities and competition in shallower, oxygenated areas, (c) direct physiological stress: decrease in food intake due to a lack of energy, and (d) scarcity of benthic food: reduced benthic productivity and biodiversity. Illustrated by the author. Fish illustration from Muus et al. (1999).

In ideal conditions with no oxygen depletion, benthos is ubiquitously available as food for both juveniles in coastal, shallower areas and deeper dwelling adult cod, all in good body condition (Figure 21a). For our data, this seemed to be the case for both juveniles and adults. It has been previously shown that the presence of hypoxic areas can affect cod condition via three different mechanisms: habitat compression, leading to crowding and strong competition in shallower, oxygenated areas (Oeberst 2008) (Figure 21b), direct physiological stress, decreasing the food intake due to a lack of energy (Teschner et al. 2010) (Figure 21c) or scarcity of benthic food due to the habitat loss for benthic fauna (Conley et al. 2009) (Figure 21d) (Casini et al. 2016). However, based on my findings, I cannot answer the question whether the 2014 MBI event has increased benthos availability, and thus cod condition. Nevertheless, the found positive trend of K_n with an increasing benthos proportion in the diet, suggests that there may be a causality.

These findings demonstrate the complexity of cod condition and highlight the importance of further studies focusing on cod condition in relation to interspecific density dependent processes, and should take both consumer and prey abundance data, stomach content and stable isotope data into account.

(4) Interspecific competition between cod and whiting

In the western Baltic Sea, whiting is very abundant and feeds predominantly on clupeids, such as the top predator cod, yet little is known about the predatory significance of whiting and its ecological role in this area (Ross et al. 2013, Ross et al. 2016).

My analysis of the trophic dynamics of these two piscivore predators showed feeding on a higher trophic level and a stronger benthic-pelagic shift in whiting. These differences explain the overall surprisingly low niche overlap, given the similar niches described for the two predators in the literature (Ross et al. 2013, Ross et al. 2016). Overall, cod displayed larger SEAc, i.e., isotopic niche spaces, than whiting, suggesting a more variable diet, in contrast to a more differentiated diet found in whiting. Taking this into account in addition to the higher trophic level displayed by whiting, and the low benthos component in its diet indicated by the high $\delta^{34}S$ values in this study, this points to a feeding strategy largely targeting pelagic fishes in the Baltic ecosystem. These findings correspond to previous results by Ross et al. (2016), which showed that clupeids make up 90% of the diet of whiting, highlighting its underestimated role as fish predator in the western Baltic Sea. In contrast, the high $\delta^{34}S$ range found in cod indicates the existence of a larger variability in prey items compared to whiting. This suggests that adult cod consume a substantial amount of benthic food resources in

addition to pelagic fish prey (Bagge et al. 1994). It can be assumed, that different feeding strategies may become even more important for cod in areas of hypoxia, where density dependent processes play a role (Casini et al. 2016). However, to assess whether the build-up of different isotopic niches may be a potential adjustment of cod to hypoxia, requires further investigations. Besides, the fact that both fish predators display an ontogenetic diet shift from benthic to pelagic prey, raises the question whether juvenile cod and whiting, that predominantly feed on benthic invertebrates (Ross et al. 2016), may potentially compete for food. This question cannot be answered here, and more data on juvenile fish is needed.

The observed differences in isotopic niche space widths showed that whiting largely targets pelagic fishes, whereby cod feeds on a larger variety of prey resources, including pelagic fishes and a substantial part of benthos. These findings explain the surprisingly low niche overlap. However, further studies are needed to assess the potential of interspecific competition for different size-classes and should include both predator and prey abundance data, as well as use SCA and SIA complementarily. Whiting is only subject to a small targeted demersal trawl fishery in the western Baltic Sea, yet its predatory importance and potential competition with the commercially important cod shows that it should be included in multispecies stock assessments.

(5) Interspecific competition between herring, sprat and three-spined stickleback

Recently, the abundance of the three-spined stickleback has drastically increased in the Baltic Proper (Ljunggren et al. 2010). It is assumed to play a considerable role in the pelagic food web as a potential competitor of the two main planktivores, herring and sprat (Jakubavičiūtė et al. 2017b), yet still only little is known about their competitive interactions.

My analysis of the trophic dynamics of the three planktivorous species showed surprisingly little evidence for an isotopic niche overlap, despite the similar diet preferences and strong diet overlap shown by Jakubavičiūtė et al. (2017b). The found differences between species and small isotopic niche overlap may be a result of sampled fish sizes, that do not overlap. Consequently, species differ in mouth size, and do not have access to similar sized prey items. Therefore, the potential of interspecific competition is here difficult to assess, and more data on different size classes is required. The most interesting finding in the analysis were the differences in SEAc sizes. Herring displayed the largest SEAc, i.e. largest isotopic niche space, indicating a greater variety of prey resources, compared to sprat and three-spined stickleback displaying smaller niche spaces. These results would be consistent with previous reports, showing that large herring (TL >15-20cm) prey on nektobenthos (mysids, amphipods

and polychaetes) and zooplankton (Casini et al. 2004), in contrast to all sized sprat and small three-spined stickleback (TL < 6.5cm), which are known to be strict zooplanktivorous, primarily feeding on calanoid copepods and cladocerans (Jakubavičiūtė et al. 2017b). It has been shown that the diet composition of the three-spined stickleback changes with increasing fish size to a more benthic diet consisting of amphipods, gastropods and isopods (Jakubavičiūtė et al. 2017a), yet due the small sized fish sample in this study, this variety in prey items cannot be displayed by the isotopic niche space. The surprising stronger pelagic signature of the three-spined stickleback, in comparison to sprat, suggests a different diet composition. A previous study by Candolin et al. (2015) has shown that three-spined sticklebacks also feed on insect larvae, which could explain the stronger pelagic signature. Surprisingly, this study did not show a feeding niche overlap between sprat and herring, as small sized herring (TL < 15cm), known to also be strictly zooplanktivorous, were not sampled.

My results demonstrated little evidence for interspecific competition, which may have been a result of different sized fish samples. Therefore, future studies should focus on a broader range of size classes, and combine both SCA and SIA.

(6) Interspecific competition between dab, flounder and plaice

The Baltic flatfish species dab, flounder and plaice are of ecological and economic importance (Florin 2005) and show high abundances in the western Baltic Sea, where they are very likely to compete for food resources. However, studies on their trophic dynamics, in particular on the potential of interspecific competition, are lacking.

My data showed a large overlap of isotopic niche spaces of dab, flounder and plaice, which suggests a high potential for interspecific competition within the flatfish community. Flounder displayed the largest isotopic niche space, indicating a high intraspecific variability. This would confirm the presence of different feeding strategies, concentrating on a benthic, pelagic, or mixed diet, allowing flounder to live in different habitats with different food availability (Mulicki 1947, Summers 1980). Adult flounder are known to mainly feed on benthic invertebrates, such as polychaetes, bivalves and crustaceans (Molander 1964, Arntz & Finger 1981), but complete their diet with fish, which would explain the large variability of $\delta^{34}S$ ratios found in flounder. In contrast to flounder, dab and plaice displayed smaller isotopic niche spaces, indicating a less variable diet. However, previous observations showed that dab and plaice do not only feed on benthic invertebrates (Arntz & Finger 1981), but also on small fishes such as sand eels (Hoeines & Bergstad 2002). However, it has to be noted that this

study only covers a small range of sizes, which may explain the surprisingly smaller isotopic niches.

Overall, my analyses revealed a strong overlap between the three flatfish species, leading to the assumption that they show a high potential for competitive interactions in the western Baltic Sea. Flounder showed the highest intraspecific variability in isotopic signatures, suggesting that they are able to use a broad spectrum of different food resources. Further research is required to investigate the diet overlap between different size-classes and also include data of other abundant flatfish species in the western Baltic Sea.

Conclusion

The main goal of the current study was to elucidate the trophic dynamics of Baltic fish species based on SIA after the 2014 MBI event. My results broadly support previous feeding ecology studies on Baltic species, yet also provide surprising insights into the trophic dynamics and isotopic niches of both commercial and non-commercial Baltic fish species, that are not routinely assessed. In particular sulphur data provided the most informative insights, and further studies should therefore focus on S, especially for the assessment of benthic-pelagic diet shifts. For routine monitoring programs, SIA could be used in a relatively convenient and logistically easy way, allowing for a high resolution, which is needed in the spatio-temporally variable environment of the Baltic Sea. Furthermore, ideally, SIA and SCA should be used complementarily in further studies, in combination with consumer and prey abundance data. A broad range of fish size classes is required to better display ontogenetic diet shifts and size classes likely to compete for food resources. This work offers valuable insights into the trophic dynamics of Baltic fish species. Thus, it demonstrates the potential of SIA to routinely assess the overall Baltic food web, demonstrated by the spatially resolved data set for both commercial and non-commercial fish species provided by a single research cruise.

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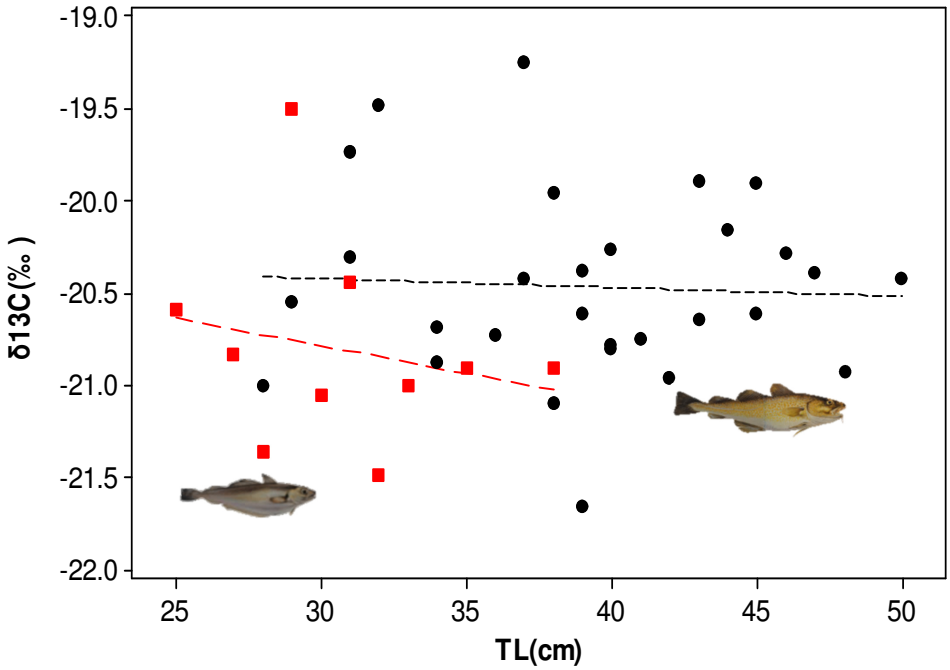
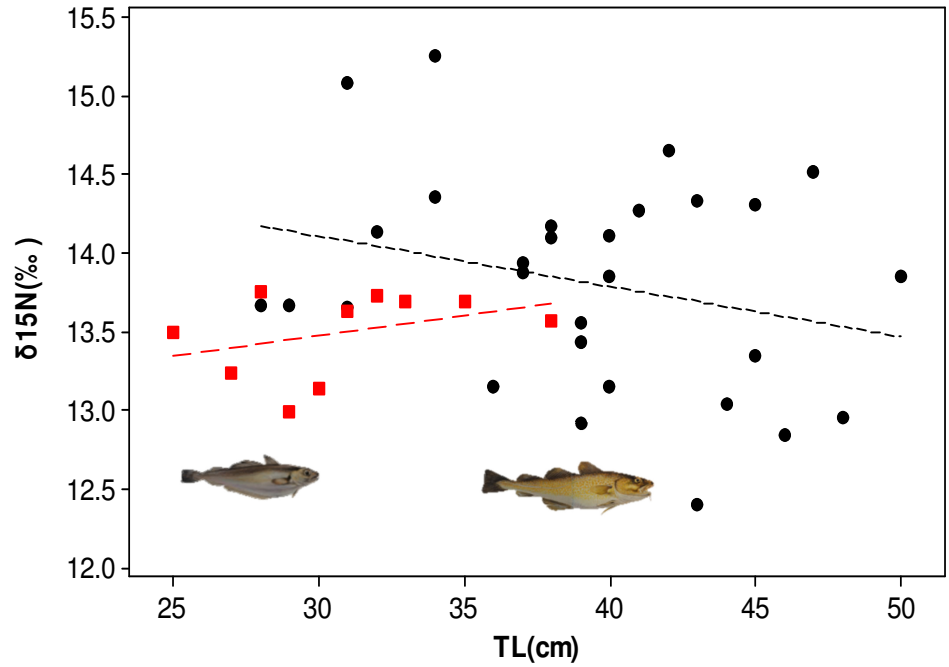
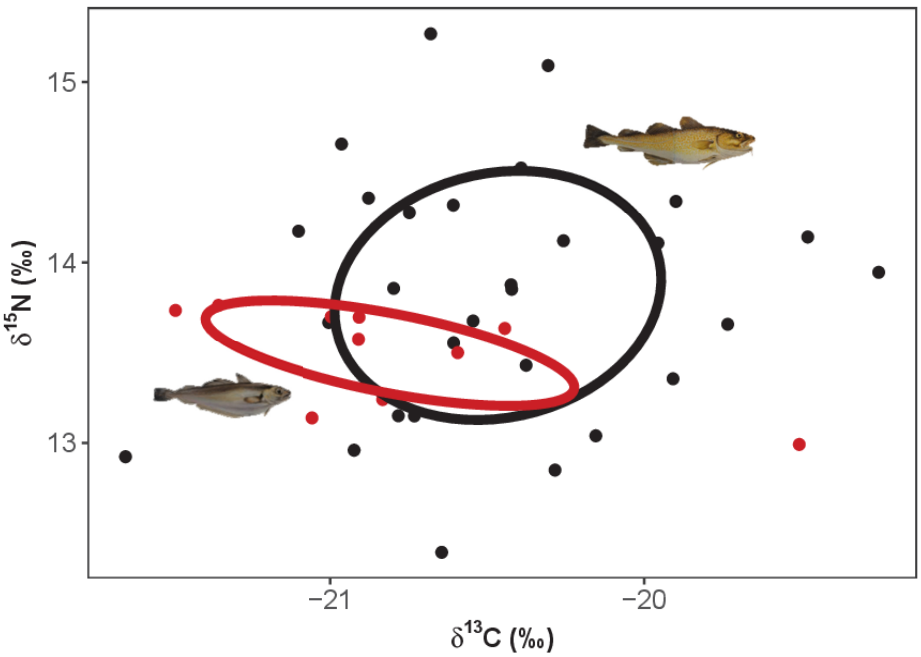
APPENDIX – Appendix 1 - Figures



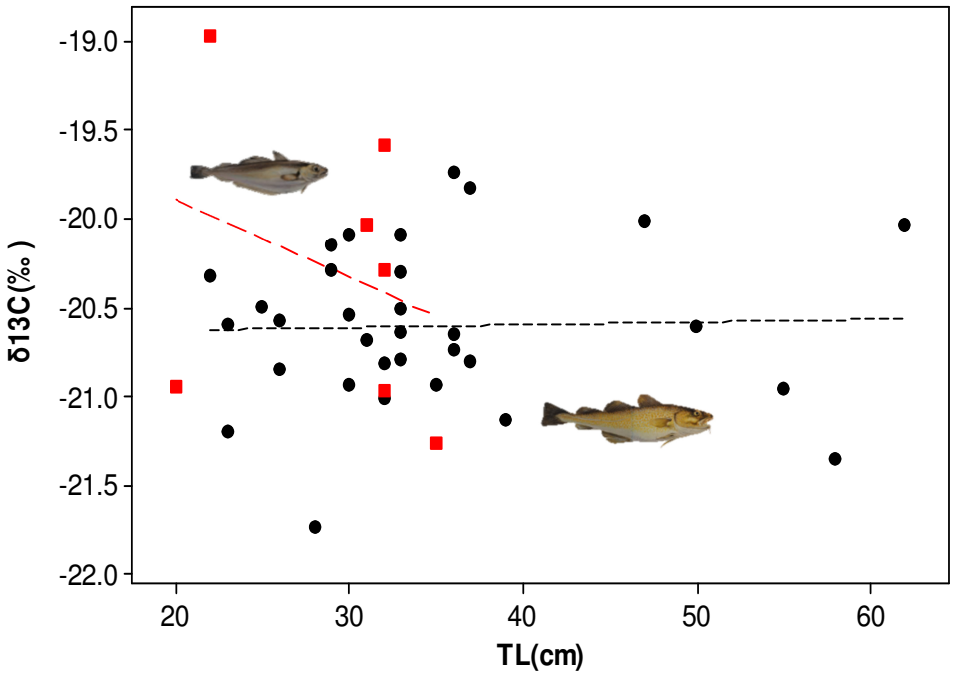
Appendix 1.1. Scatterplot of $\delta^{13}C$ (‰) and TL (cm) for cod and whiting of SD24 – Arkona Basin; dotted lines represent regression lines; ● cod, ■ whiting. Fish illustrations from Muus et al. (1999).



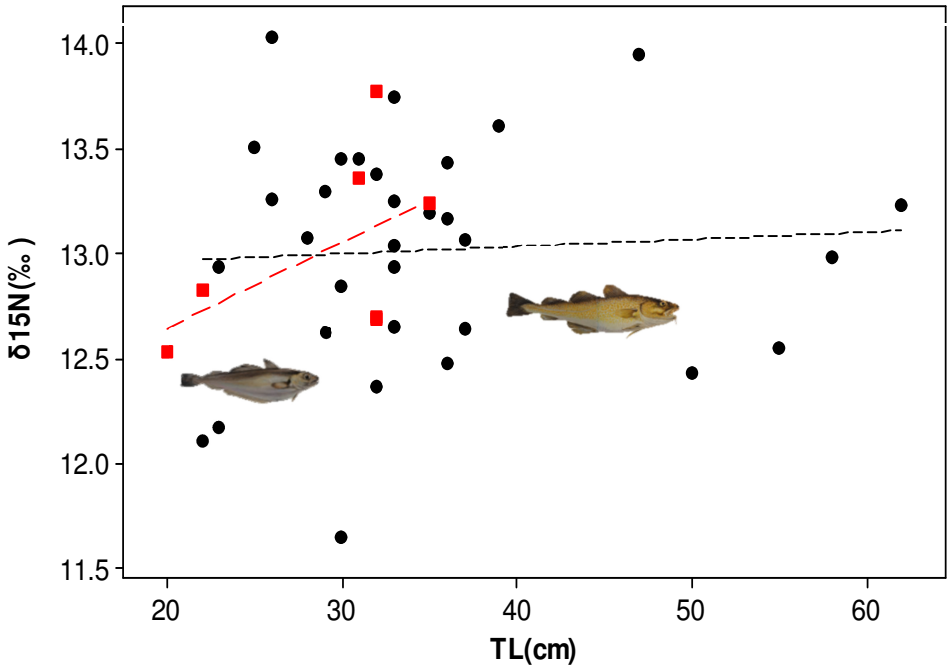
Appendix 1.2. Scatterplot of $\delta^{15}N$ (‰) and TL (cm) for cod and whiting of SD24 – Arkona Basin; dotted lines represent regression lines; ● cod, ■ whiting. Fish illustrations from Muus et al. (1999).



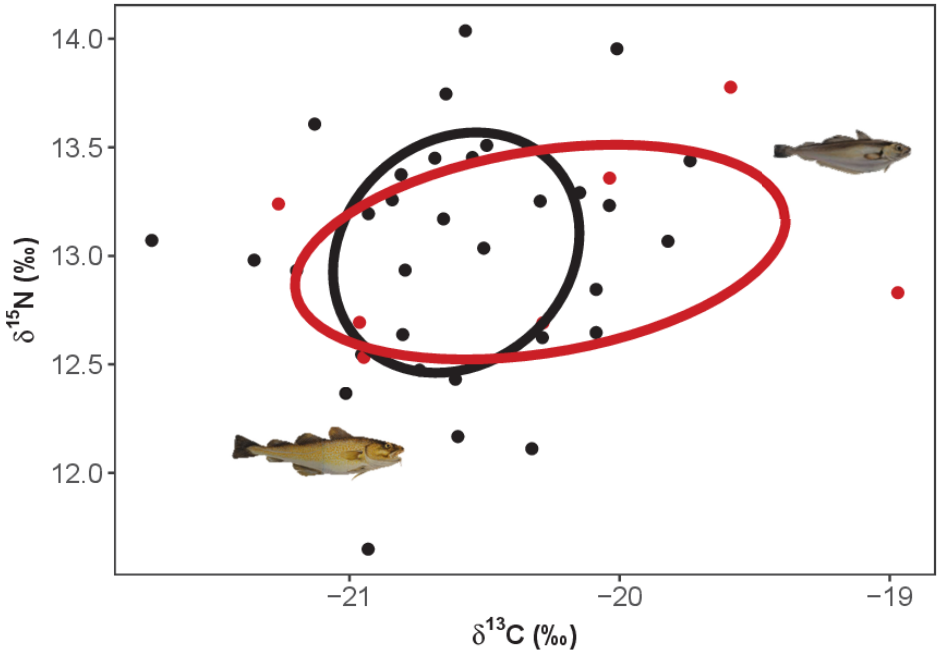
Appendix 1.3. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) between cod and whiting of SD24 – Arkona Basin; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; ● cod, ● whiting. Fish illustrations from Muus et al. (1999).



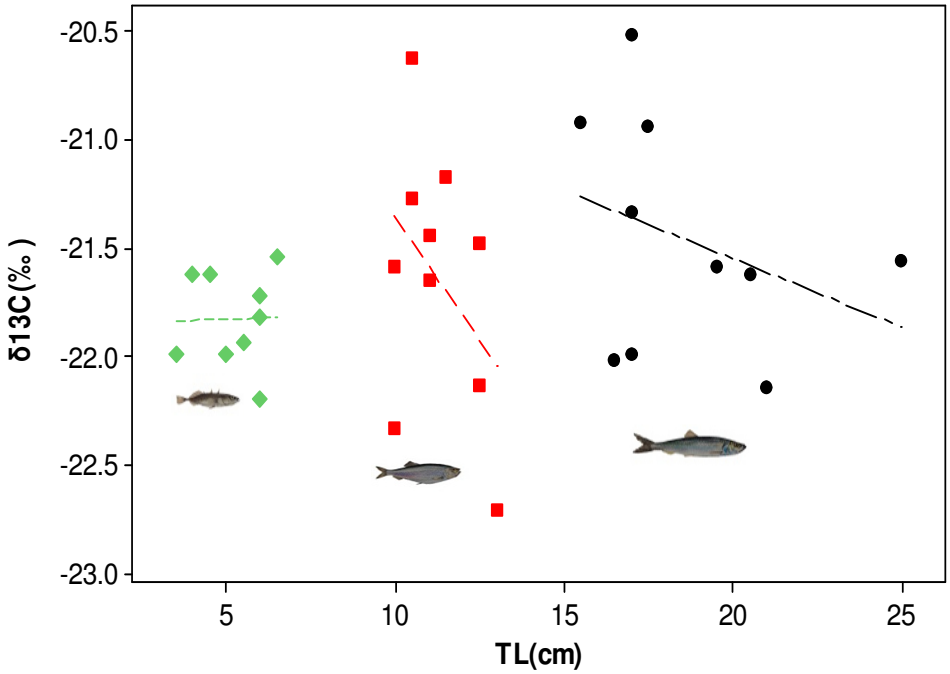
Appendix 1.4. Scatterplot of $\delta^{13}C$ (‰) and TL (cm) for cod and whiting of SD25 – Bornholm Basin; dotted lines represent regression lines; ● cod, ■ whiting. Fish illustrations from Muus et al. (1999).



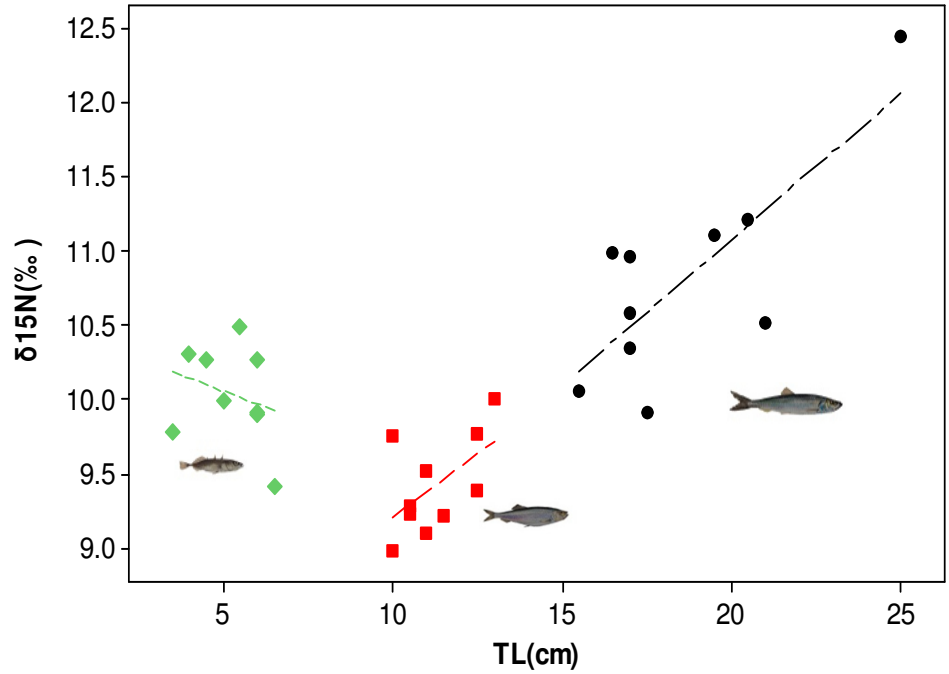
Appendix 1.5. Scatterplot of $\delta^{15}N$ (‰) and TL (cm) for cod and whiting of SD25 – Bornholm Basin; dotted lines represent regression lines; ● cod, ■ whiting. Fish illustrations from Muus et al. (1999).



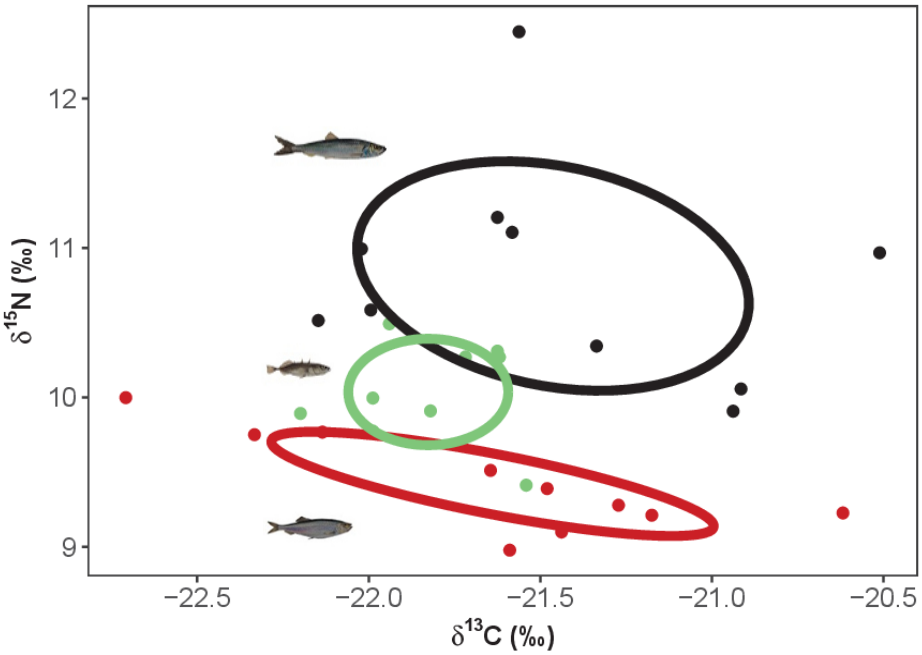
Appendix 1.6. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) between cod and whiting of SD25 – Bornholm Basin; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; ● cod, ● whiting. Fish illustrations from Muus et al. (1999).



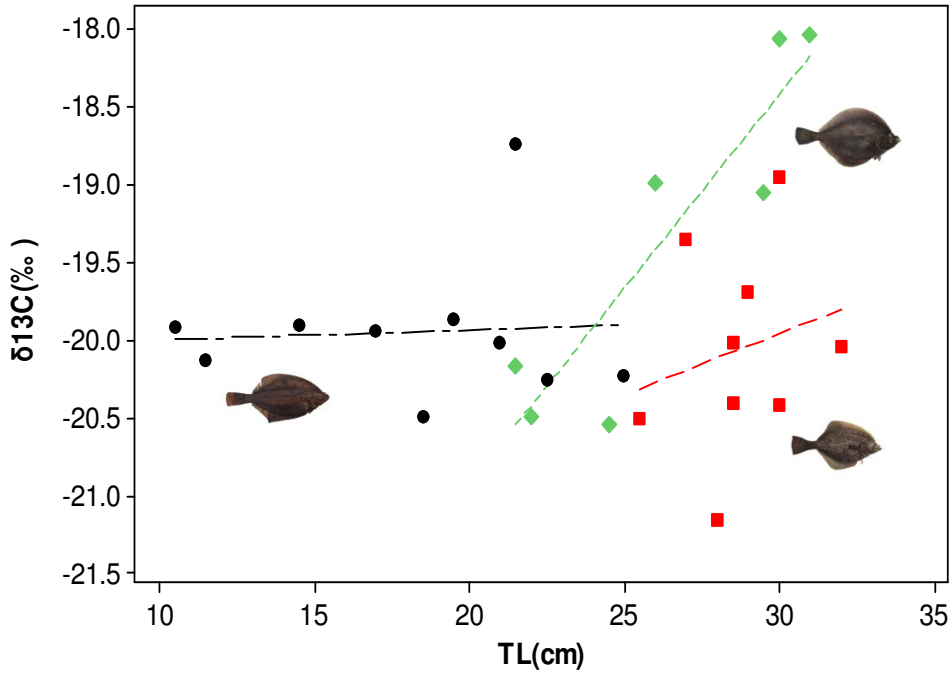
Appendix 1.7. Scatterplot of $\delta^{13}C$ (‰) and TL (cm) for herring, sprat and three-spined stickleback of SD25 – Bornholm Basin; dotted lines represent regression lines; ● herring, ■ sprat, ◆ three-spined stickleback. Fish illustrations from Muus et al. (1999).



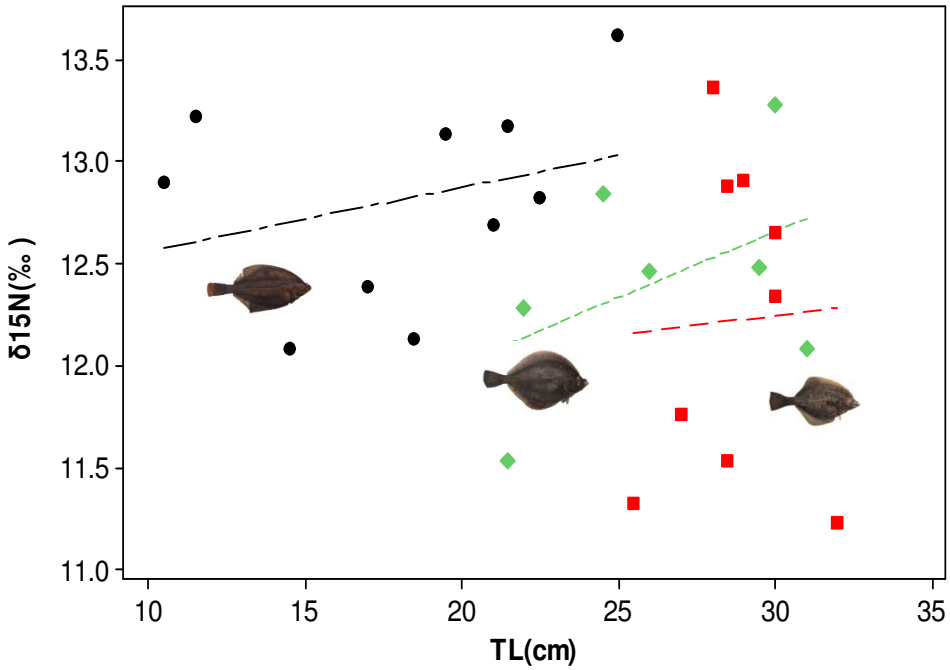
Appendix 1.8. Scatterplot of $\delta^{15}N$ (‰) and TL (cm) for herring, sprat and three-spined stickleback of SD25 – Borhnholm Basin; dotted lines represent regression lines; ● herring, ■ sprat, ◆ three-spined stickleback. Fish illustrations from Muus et al. (1999).



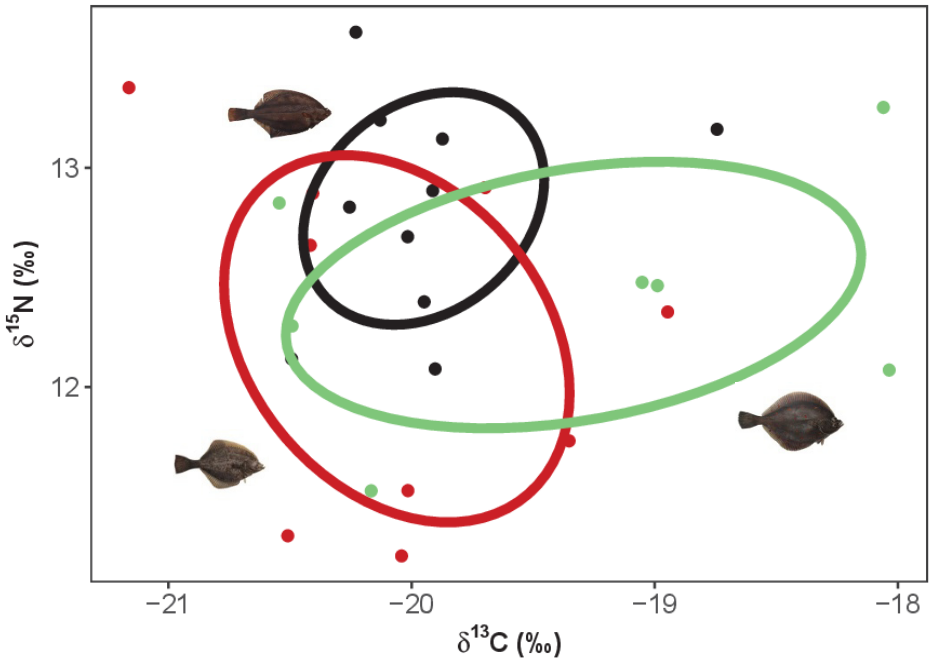
Appendix 1.9. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) between herring, sprat and three-spined stickleback of SD25 – Bornholm Basin; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; ● herring, ● sprat, ● three-spined stickleback. Fish illustrations from Muus et al. (1999).



Appendix 1.10. Scatterplot of $\delta^{13}C$ (‰) and TL (cm) for dab, flounder and plaice of SD22 – Kiel Bight; dotted lines represent regression lines; ● dab, ■ flounder, ◆ plaice. Fish illustrations from Muus et al. (1999).



Appendix 1.11. Scatterplot of $\delta^{15}N$ (‰) and TL (cm) for dab, flounder and plaice of SD22 – Kiel Bight; dotted lines represent regression lines; ● dab, ■ flounder, ◆ plaice. Fish illustrations from Muus et al. (1999).



Appendix 1.12. Isotopic niche overlap of $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) between dab, flounder and plaice of SD22 – Kiel Bight; standard ellipse areas for small sample sizes (SEAc) representing isotopic niches are depicted using solid lines; ● dab, ● flounder, ● plaice. Fish illustrations from Muus et al. (1999).

APPENDIX – Appendix 2 - Tables

Appendix 2.1. Overview of all statistical models run in MINITAB (Minitab Incorporated; State College, USA, version 14). SD22 – Kiel Bight, SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

Type	**Model**	**Species**	**SD**	**Parameters**		
				Response variable	**Explanatory variable(s)**	**Covariate**
ANCOVA GLM	$\delta^{13}C$ ~ SD,TL,SD*TL	cod	24,25,26	$\delta^{13}C$	SD, TL,SD*TL	TL
	$\delta^{15}N$ ~ SD,TL,SD*TL	cod	24,25,26	$\delta^{15}N$	SD, TL,SD*TL	TL
	$\delta^{34}S$ ~ SD,TL,SD*TL	cod	24,25,26	$\delta^{34}S$	SD, TL,SD*TL	TL
	K_n ~ SD,$\delta^{34}S$,SD*$\delta^{34}S$	cod	24,25,26	K_n	SD,$\delta^{34}S$,SD* $\delta^{34}S$	$\delta^{34}S$
	$\delta^{13}C$ ~ SD,species,SD*species,TL	gadids	24,25	$\delta^{13}C$	SD,species,SD*species, TL	TL
	$\delta^{15}N$ ~ SD,species,SD*species,TL	gadids	24,25	$\delta^{15}N$	SD,species,SD*species, TL	TL
	$\delta^{34}S$ ~ SD,species,SD*species,TL	gadids	24,25	$\delta^{34}S$	SD,species,SD*species, TL	TL
	$\delta^{13}C$ ~ species,TL,species*TL	flatfish	22	$\delta^{13}C$	species,TL,species*TL	TL
	$\delta^{15}N$ ~ species,TL,species*TL	flatfish	22	$\delta^{15}N$	species,TL,species*TL	TL
	$\delta^{34}S$ ~ species,TL,species*TL	flatfish	22	$\delta^{34}S$	species,TL,species*TL	TL
ANOVA GLM	$\delta^{13}C$ ~ species	pelagic fish	25	$\delta^{13}C$	species	-
	$\delta^{15}N$ ~ species	pelagic fish	25	$\delta^{15}N$	species	-
	$\delta^{34}S$ ~ species	pelagic fish	25	$\delta^{34}S$	species	-

Appendix 2.2. Overview of SIA results of all 296 samples. SD22 – Kiel Bight, SD24 – Arkona Basin, SD25 – Bornholm Basin, SD26 – Gdansk Deep.

SD	Station	Species	TL (cm)	Weight (g)	Gutted weight (g)	Kn	Corr. $\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Corr. $\delta^{34}S$ (‰)	C:N ratio
22	KB06	American plaice	20.0	42.0	*	*	-20.002	13.768	11.852	3.952
24	H26	Blue mussel	5.4	9.5	*	*	-20.914	7.785	15.086	4.395
24	H26	Blue mussel	5.0	7.0	*	*	-19.735	6.912	16.406	4.535
24	H26	Blue mussel	3.9	3.6	*	*	-20.780	6.721	16.337	4.698
24	H26	Blue mussel	4.3	4.0	*	*	-20.487	7.833	15.754	4.735
24	H26	Blue mussel	2.4	0.7	*	*	-20.692	6.569	15.331	4.587
22	KB06	Cod	25.0	127.0	115.0	0.97	-20.410	14.858	11.947	3.774
24	H19	Cod	44.0	902.0	653.0	1.02	-20.154	13.039	14.907	3.903
24	H19	Cod	48.0	936.0	798.0	0.96	-20.924	12.959	15.387	3.779
24	H19	Cod	38.0	633.0	527.0	1.27	-21.101	14.173	15.513	3.809
24	H19	Cod	46.0	811.0	670.0	0.91	-20.284	12.849	15.215	3.823
24	H19	Cod	43.0	777.0	580.0	0.97	-20.645	12.393	15.744	3.778
24	H19	Cod	45.0	1084.0	857.0	1.25	-19.908	13.355	14.940	3.898
24	H19	Cod	50.0	1145.0	965.0	1.03	-20.422	13.851	15.226	3.832
24	H19	Cod	34.0	377.0	331.0	1.12	-20.680	15.267	12.870	3.958
24	H19	Cod	39.0	681.0	542.0	1.21	-21.652	12.923	15.156	3.856
24	H19	Cod	40.0	553.0	430.0	0.89	-20.257	14.120	14.286	3.922
24	H19	Cod	31.0	312.0	253.0	1.13	-19.734	13.657	12.854	4.040
24	H19	Cod	37.0	377.0	312.0	0.82	-20.424	13.876	12.419	3.927
24	H19	Cod	29.0	245.0	198.0	1.08	-20.545	13.675	12.214	3.928
24	H24	Cod	38.0	548.0	459.0	1.11	-19.956	14.107	13.080	3.858
24	H24	Cod	39.0	522.0	459.0	1.03	-20.376	13.430	14.669	3.902
24	H24	Cod	28.0	225.0	198.0	1.19	-21.005	13.667	11.769	3.819
24	H24	Cod	40.0	632.0	506.0	1.05	-20.783	13.150	13.546	4.025
24	H25	Cod	45.0	905.0	746.0	1.09	-20.608	14.317	13.330	3.847

24	H25	Cod	39.0	558.0	435.0	0.97	-20.607	13.554	14.344	3.816
24	H25	Cod	32.0	289.0	244.0	0.99	-19.479	14.141	13.589	3.832
24	H25	Cod	42.0	800.0	714.0	1.28	-20.964	14.656	13.920	3.904
24	H25	Cod	36.0	446.0	361.0	1.03	-20.732	13.149	13.919	3.842
24	H25	Cod	43.0	685.0	574.0	0.96	-19.896	14.336	14.190	3.823
24	H25	Cod	31.0	290.0	250.0	1.11	-20.306	15.091	12.919	3.966
24	H25	Cod	37.0	489.0	451.0	1.18	-19.253	13.945	14.108	3.849
24	H25	Cod	34.0	407.0	348.0	1.17	-20.878	14.356	13.429	3.814
24	H25	Cod	41.0	710.0	624.0	1.20	-20.748	14.276	12.111	3.791
24	H25	Cod	47.0	952.0	875.0	1.12	-20.392	14.523	15.038	3.798
24	H25	Cod	41.0	592.0	505.0	0.97	-20.656	10.616	14.412	3.925
24	H25	Cod	40.0	772.0	601.0	1.25	-20.798	13.856	14.091	3.762
24	H25	Cod	28.0	192.0	168.0	1.01	-20.828	10.832	15.067	3.837
25	BB17	Cod	62.0	2123.0	1190.0	0.66	-20.038	13.232	15.950	3.812
25	BB17	Cod	58.0	1700.0	1172.0	0.80	-21.353	12.980	15.528	3.798
25	BB17	Cod	50.0	1154.0	895.0	0.95	-20.608	12.431	15.322	3.966
25	BB17	Cod	39.0	568.0	446.0	1.00	-21.129	13.607	14.950	4.004
25	BB17	Cod	55.0	1522.0	1094.0	0.87	-20.955	12.545	16.005	3.795
25	BB17	Cod	37.0	580.0	452.0	1.18	-20.803	12.637	15.376	3.864
25	BB17	Cod	31.0	291.0	271.0	1.21	-20.684	13.450	11.578	4.051
25	BB17	Cod	29.0	307.0	232.0	1.26	-20.148	13.291	12.174	4.067
25	BB17	Cod	32.0	196.0	155.0	0.63	-20.809	13.374	12.876	3.910
25	BB17	Cod	26.0	218.0	174.0	1.31	-20.842	13.258	12.167	3.901
25	BB17	Cod	30.0	170.0	137.0	0.67	-20.087	12.845	11.822	3.914
25	BB17	Cod	29.0	211.0	167.0	0.91	-20.286	12.623	14.923	3.974
25	BB17	Cod	25.0	146.0	130.0	1.10	-20.492	13.509	11.568	3.955
25	BB17	Cod	23.0	107.0	94.0	1.02	-21.196	12.932	13.713	3.853
25	BB29	Cod	30.0	250.0	201.0	0.99	-20.931	11.648	15.580	3.996
25	BB29	Cod	33.0	372.0	287.0	1.06	-20.087	12.646	14.610	3.915

25	BB29	Cod	26.0	140.0	121.0	0.91	-20.571	14.037	13.079	3.831
25	BB29	Cod	33.0	310.0	243.0	0.90	-20.503	13.035	13.447	4.049
25	BB29	Cod	23.0	106.0	89.0	0.97	-20.599	12.167	14.779	4.018
25	BB29	Cod	22.0	93.0	80.0	0.99	-20.325	12.111	14.808	3.832
25	BB29	Cod	36.0	507.0	309.0	0.88	-19.739	13.438	16.359	4.043
25	BB29	Cod	28.0	192.0	173.0	1.04	-21.732	13.071	14.146	4.056
25	BB29	Cod	33.0	333.0	271.0	1.00	-20.794	12.934	15.201	4.064
25	BB29	Cod	25.0	140.0	117.0	0.99	-20.145	14.034	7.446	4.019
25	BB29	Cod	33.0	308.0	249.0	0.92	-20.643	13.746	15.106	3.929
25	BB40	Cod	36.0	431.0	334.0	0.95	-20.741	12.473	14.616	3.821
25	BB40	Cod	36.0	369.0	304.0	0.86	-20.652	13.170	11.630	3.932
25	BB40	Cod	33.0	356.0	244.0	0.90	-20.294	13.252	14.596	3.850
25	BB40	Cod	32.0	271.0	218.0	0.88	-21.011	12.361	14.948	3.914
25	BB40	Cod	30.0	226.0	211.0	1.04	-20.545	13.453	15.908	3.850
25	BB40	Cod	37.0	441.0	355.0	0.93	-19.821	13.067	15.562	3.844
25	BB40	Cod	35.0	354.0	295.0	0.91	-20.930	13.194	14.842	3.810
25	BB40	Cod	47.0	1159.0	779.0	1.00	-20.010	13.954	14.554	3.744
26	GD57	Cod	60.0	2036.0	1387.0	0.85	-21.158	13.399	15.131	3.951
26	GD57	Cod	48.0	1100.0	756.0	0.91	-20.329	13.784	14.767	4.061
26	GD57	Cod	35.0	440.0	312.0	0.97	-20.053	13.687	14.250	3.909
26	GD57	Cod	42.0	775.0	600.0	1.08	-19.880	12.663	15.988	3.922
26	GD57	Cod	30.0	206.0	179.0	0.88	-20.430	13.077	14.302	3.983
26	GD57	Cod	33.0	404.0	292.0	1.08	-20.414	13.955	12.092	3.852
26	GD57	Cod	40.0	714.0	551.0	1.14	-20.612	12.432	14.557	3.815
26	GD57	Cod	47.0	1021.0	782.0	1.00	-20.974	12.757	14.737	3.771
26	GD57	Cod	32.0	337.0	257.0	1.04	-21.221	13.078	14.143	3.788
26	GD57	Cod	28.0	203.0	162.0	0.98	-21.117	12.312	14.459	3.926
26	GD57	Cod	39.0	488.0	388.0	0.87	-20.048	12.797	14.147	3.823
26	GD57	Cod	33.0	379.0	284.0	1.05	-20.205	12.569	14.729	3.905

26	GD57	Cod	27.0	185.0	147.0	0.99	-19.874	14.685	13.144	3.934
26	GD57	Cod	30.0	274.0	222.0	1.09	-20.477	12.348	14.634	3.924
26	GD57	Cod	42.0	797.0	570.0	1.02	-21.227	13.981	13.572	3.879
26	GD60	Cod	5.8	*	*	0.00	-20.988	13.507	13.098	3.844
26	GD60	Cod	37.0	408.0	335.0	0.88	-20.139	13.484	12.840	3.856
26	GD60	Cod	42.0	720.0	524.0	0.94	-20.560	12.269	14.551	3.816
26	GD60	Cod	36.0	476.0	396.0	1.13	-20.465	13.201	11.939	3.897
26	GD60	Cod	46.0	826.0	720.0	0.98	-20.878	13.687	14.249	3.783
26	GD60	Cod	42.0	850.0	569.0	1.02	-19.484	12.882	15.401	3.952
26	GD60	Cod	41.0	635.0	490.0	0.94	-20.146	13.449	14.059	3.991
26	GD60	Cod	49.0	1025.0	842.0	0.95	-20.755	14.649	14.857	3.830
26	GD60	Cod	39.0	474.0	402.0	0.90	-20.407	12.947	14.567	3.873
26	GD60	Cod	33.0	366.0	289.0	1.07	-19.947	13.948	14.057	3.973
26	GD60	Cod	40.0	549.0	447.0	0.93	-20.306	12.316	16.035	3.959
26	GD60	Cod	28.0	213.0	189.0	1.14	-20.380	13.188	14.047	3.894
26	GD60	Cod	44.0	1084.0	746.0	1.16	-20.961	13.249	14.372	3.897
26	GD60	Cod	34.0	327.0	270.0	0.91	-20.788	12.982	14.301	3.841
26	GD60	Cod	31.0	304.0	255.0	1.13	-20.221	14.274	13.930	3.914
26	GD60	Cod	31.0	320.0	248.0	1.10	-20.433	13.420	13.438	3.928
22	KB06	Common starfish	12.4	20.0	*	*	-17.852	10.914	14.763	5.454
22	KB06	Common starfish	5.5	2.8	*	*	-18.250	10.810	14.635	4.809
22	KB06	Common starfish	8.4	8.8	*	*	-17.765	12.583	13.585	4.946
22	KB06	Common starfish	9.4	12.5	*	*	-18.724	11.181	14.465	5.651
22	KB06	Common starfish	7.1	5.8	*	*	-18.373	11.069	13.648	4.703
24	H25	Common starfish	5.6	9.3	*	*	-17.265	8.450	16.686	5.820
24	H25	Common starfish	7.6	11.4	*	*	-18.141	10.314	17.787	5.478
24	H25	Common starfish	6.4	9.4	*	*	-17.763	9.452	17.704	5.881
24	H25	Common starfish	5.9	6.1	*	*	-19.040	9.591	16.151	5.077
24	H25	Common starfish	5.2	5.3	*	*	-18.728	9.806	16.152	5.196

22	KB06	Dab	14.5	32.0	*	*	-19.903	12.083	13.023	3.999
22	KB06	Dab	17.0	54.0	*	*	-19.948	12.389	11.439	3.980
22	KB06	Dab	18.5	66.0	*	*	-20.493	12.129	15.455	4.012
22	KB06	Dab	11.5	14.0	*	*	-20.129	13.218	14.851	4.031
22	KB06	Dab	19.5	80.0	*	*	-19.873	13.132	11.037	4.021
22	KB06	Dab	10.5	12.0	*	*	-19.913	12.896	13.911	4.088
22	KB06	Dab	21.5	114.0	*	*	-18.744	13.176	11.114	4.181
22	KB06	Dab	22.5	120.0	*	*	-20.255	12.821	12.192	4.091
22	KB06	Dab	21.0	88.0	*	*	-20.016	12.686	13.447	4.010
22	KB06	Dab	25.0	164.0	*	*	-20.229	13.619	10.084	4.076
24	H25	Dab	21.0	112.0	*	*	-20.284	12.002	13.484	4.148
24	H26	Dab	26.5	212.0	*	*	-19.419	12.893	11.462	5.061
22	KB06	Flounder	28.0	236.0	*	*	-21.162	13.366	11.637	4.108
22	KB06	Flounder	30.0	278.0	*	*	-20.416	12.647	10.113	4.147
22	KB06	Flounder	28.5	222.0	*	*	-20.406	12.884	11.170	3.944
22	KB06	Flounder	32.0	326.0	*	*	-20.041	11.230	13.053	3.938
22	KB06	Flounder	28.5	242.0	*	*	-20.015	11.528	8.130	4.013
22	KB06	Flounder	27.0	190.0	*	*	-19.352	11.755	9.419	4.162
22	KB06	Flounder	28.5	232.0	*	*	-18.896	17.386	12.752	4.092
22	KB06	Flounder	25.5	180.0	*	*	-20.509	11.322	5.712	4.053
22	KB06	Flounder	30.0	280.0	*	*	-18.947	12.343	11.167	3.793
22	KB06	Flounder	29.0	220.0	*	*	-19.697	12.910	9.567	3.888
24	H19	Flounder	37.0	397.0	*	*	-12.527	11.193	13.592	4.013
24	H19	Flounder	25.5	176.0	*	*	-21.025	11.114	13.099	4.241
24	H25	Flounder	27.0	196.0	*	*	-20.544	9.882	13.635	4.353
24	H25	Flounder	23.5	136.0	*	*	-20.817	12.104	12.554	4.085
24	H26	Flounder	19.0	78.0	*	*	-17.548	15.045	7.910	3.954
25	BB29	Flounder	27.5	202.0	*	*	-23.636	11.826	14.262	4.151
25	BB29	Flounder	25.5	142.0	*	*	-19.992	11.170	14.803	4.038

25	BB29	Flounder	26.0	164.0	*	*	-18.955	12.353	13.815	4.147
25	BB29	Flounder	26.0	176.0	*	*	-21.545	12.037	13.502	4.236
25	BB29	Flounder	21.0	98.0	*	*	-19.345	12.661	13.431	4.205
25	BB29	Flounder	26.0	172.0	*	*	-20.783	9.804	14.495	4.197
25	BB29	Flounder	26.5	166.0	*	*	-20.558	10.266	12.821	4.187
25	BB29	Flounder	29.5	226.0	*	*	-18.757	10.359	14.442	4.412
25	BB29	Flounder	21.0	96.0	*	*	-21.748	12.148	13.115	4.218
26	GD57	Flounder	22.0	100.0	*	*	-20.736	13.275	10.547	4.177
26	GD57	Flounder	20.0	76.0	*	*	-19.897	14.004	13.286	4.114
26	GD57	Flounder	24.5	140.0	*	*	-21.155	12.081	11.604	3.739
26	GD57	Flounder	23.0	130.0	*	*	-20.634	13.148	9.663	3.823
26	GD57	Flounder	27.0	236.0	*	*	-20.917	12.632	12.383	3.771
26	GD57	Flounder	21.0	96.0	*	*	-19.969	13.317	10.471	4.096
26	GD57	Flounder	30.0	282.0	*	*	-21.127	12.878	12.371	3.838
26	GD57	Flounder	22.5	118.0	*	*	-20.893	14.051	4.700	4.187
26	GD57	Flounder	38.0	530.0	*	*	-20.803	13.341	11.471	4.233
26	GD57	Flounder	37.0	462.0	*	*	-20.732	12.892	11.758	3.845
22	KB06	Herring	16.5	28.4	*	*	-20.955	11.678	15.264	3.998
22	KB06	Herring	11.0	10.4	*	*	-22.081	11.015	15.216	3.912
22	KB06	Herring	16.0	29.8	*	*	-21.683	11.507	15.288	4.674
22	KB06	Herring	10.0	7.1	*	*	-21.501	14.424	14.993	4.050
22	KB06	Herring	14.0	19.3	*	*	-21.264	12.710	13.922	4.250
22	KB06	Herring	12.5	16.6	*	*	-22.009	11.638	15.071	5.064
22	KB06	Herring	9.0	5.3	*	*	-21.286	13.984	14.345	4.140
22	KB06	Herring	12.0	13.6	*	*	-21.382	11.756	14.842	4.248
22	KB06	Herring	8.0	3.7	*	*	-20.867	14.772	14.683	4.008
22	KB06	Herring	13.0	16.2	*	*	-20.857	12.561	15.630	4.362
24	H24	Herring	20.0	52.0	*	*	-22.184	12.402	16.000	3.912
24	H24	Herring	19.0	50.0	*	*	-21.000	12.788	15.500	4.088

24	H24	Herring	22.0	72.0	*	*	-22.015	12.640	15.960	3.929
24	H24	Herring	18.0	40.0	*	*	-22.992	12.931	15.513	3.883
24	H24	Herring	23.0	86.0	*	*	-22.509	13.279	14.897	4.088
24	H24	Herring	12.0	11.5	*	*	-21.218	11.502	14.783	3.958
24	H24	Herring	13.0	14.4	*	*	-20.475	10.816	14.805	4.111
24	H24	Herring	25.0	108.0	*	*	-21.904	12.867	15.063	4.947
24	H24	Herring	22.0	78.0	*	*	-21.270	13.042	15.359	4.183
24	H24	Herring	12.5	13.9	*	*	-23.618	12.379	15.648	4.272
25	BB05	Herring	25.0	122.0	*	*	-21.562	12.446	15.608	3.818
25	BB29	Herring	17.0	26.0	*	*	-21.336	10.343	15.941	3.892
25	BB29	Herring	21.0	64.0	*	*	-22.147	10.514	16.178	4.159
25	BB29	Herring	17.0	38.0	*	*	-20.511	10.967	16.304	4.144
25	BB29	Herring	17.0	30.0	*	*	-21.994	10.584	15.448	4.117
25	BB29	Herring	20.5	48.0	*	*	-21.625	11.204	15.184	3.863
25	BB29	Herring	19.5	42.0	*	*	-21.582	11.104	14.889	3.944
25	BB29	Herring	17.5	42.0	*	*	-20.938	9.907	16.925	4.007
25	BB29	Herring	16.5	36.0	*	*	-22.021	10.993	17.439	4.230
25	BB29	Herring	15.5	36.0	*	*	-20.915	10.056	15.601	3.903
26	GD57	Herring	20.0	46.0	*	*	-20.354	11.083	15.630	4.608
26	GD57	Herring	22.5	66.0	*	*	-21.432	11.162	16.975	4.305
26	GD57	Herring	22.5	60.0	*	*	-20.318	12.454	15.907	4.504
26	GD57	Herring	17.0	22.0	*	*	-19.936	10.862	16.044	4.549
26	GD57	Herring	17.5	34.0	*	*	-20.370	10.434	16.452	4.483
26	GD57	Herring	21.5	52.0	*	*	-20.486	11.953	16.871	4.357
26	GD57	Herring	19.0	48.0	*	*	-20.218	11.370	15.869	4.557
26	GD57	Herring	21.5	56.0	*	*	-20.241	12.162	16.311	4.492
26	GD57	Herring	19.0	40.0	*	*	-22.551	11.115	16.877	4.269
26	GD57	Herring	15.5	24.0	*	*	-20.002	9.821	15.768	3.901
22	KB06	Lumpfish	44.5	3590.0	*	*	-18.665	12.201	16.814	3.854

22	KB06	Lumpfish	41.5	2969.0	*	*	-19.376	11.051	15.761	3.515
22	KB06	Ocean quahog	4.0	20.0	*	*	-19.280	10.123	15.134	4.694
22	KB06	Ocean quahog	3.2	4.1	*	*	-18.556	9.987	14.400	4.937
22	KB06	Ocean quahog	3.3	8.4	*	*	-18.537	9.638	14.085	4.804
22	KB06	Ocean quahog	3.7	12.5	*	*	-18.480	9.993	14.486	4.768
22	KB06	Ocean quahog	3.8	15.1	*	*	-18.639	9.643	14.061	4.783
22	KB06	Plaice	21.5	108.0	*	*	-20.166	11.527	11.450	4.518
22	KB06	Plaice	24.5	164.0	*	*	-20.544	12.840	12.319	4.600
22	KB06	Plaice	22.0	120.0	*	*	-20.491	12.279	12.020	4.524
22	KB06	Plaice	26.0	166.0	*	*	-18.989	12.463	12.064	4.352
22	KB06	Plaice	30.0	262.0	*	*	-18.060	13.276	12.972	4.532
22	KB06	Plaice	29.5	250.0	*	*	-19.052	12.478	11.245	4.705
22	KB06	Plaice	31.0	280.0	*	*	-18.036	12.078	8.608	4.462
24	H25	Plaice	29.0	276.0	*	*	-19.745	10.905	14.857	3.932
24	H25	Plaice	33.0	396.0	*	*	-19.287	11.352	9.891	3.894
24	H25	Plaice	28.5	194.0	*	*	-19.327	11.987	14.310	3.817
24	H26	Plaice	45.0	987.0	*	*	-18.269	11.270	14.173	4.759
24	H26	Plaice	27.5	184.0	*	*	-18.609	11.137	13.623	4.764
24	H26	Plaice	28.5	258.0	*	*	-17.366	11.582	14.894	4.958
24	H26	Plaice	28.0	216.0	*	*	-19.364	11.208	13.852	4.882
24	H26	Plaice	28.0	264.0	*	*	-19.984	11.475	13.811	5.133
22	KB06	Red whelk	5.1	10.7	*	*	-17.147	11.742	14.880	4.780
22	KB06	Red whelk	5.8	16.1	*	*	-17.010	11.790	14.773	5.221
22	KB06	Red whelk	4.3	6.8	*	*	-17.805	10.576	16.309	5.243
25	BB40	Smelt	11.0	6.2	*	*	-20.655	11.534	14.553	3.742
22	KB06	Spotted dragonet	12.8	9.4	*	*	-19.751	13.035	11.466	4.081
22	KB06	Sprat	12.0	12.0	*	*	-21.371	11.973	15.947	5.639
22	KB06	Sprat	9.5	6.0	*	*	-21.407	10.552	16.192	5.169
22	KB06	Sprat	13.0	14.6	*	*	-21.366	12.884	17.552	5.126

22	KB06	Sprat	13.5	22.2	*	*	-21.200	11.568	15.890	4.325
22	KB06	Sprat	8.0	3.8	*	*	-22.645	11.726	14.549	4.176
22	KB06	Sprat	11.5	11.8	*	*	-21.619	11.099	17.283	4.619
22	KB06	Sprat	6.5	2.0	*	*	-21.781	12.535	15.309	5.620
22	KB06	Sprat	10.5	8.6	*	*	-22.186	11.591	15.575	4.920
22	KB06	Sprat	11.0	11.0	*	*	-22.104	12.486	16.394	4.808
22	KB06	Sprat	7.0	2.5	*	*	-21.716	13.029	15.391	4.013
24	H24	Sprat	12.0	12.6	*	*	-20.871	10.988	16.923	6.178
24	H24	Sprat	13.0	16.2	*	*	-21.183	11.504	15.802	4.414
24	H24	Sprat	12.5	15.1	*	*	-22.210	10.807	16.676	4.745
24	H24	Sprat	12.5	16.4	*	*	-22.278	10.191	17.481	4.956
24	H24	Sprat	11.5	12.0	*	*	-22.410	10.555	15.608	5.245
24	H24	Sprat	13.0	16.1	*	*	-22.393	10.279	16.881	4.716
24	H24	Sprat	11.5	12.4	*	*	-21.341	11.719	14.841	4.883
24	H24	Sprat	13.0	15.4	*	*	-21.536	10.874	15.463	4.647
24	H24	Sprat	12.0	14.2	*	*	-22.404	10.402	15.354	5.430
25	BB29	Sprat	10.5	8.2	*	*	-20.618	9.226	16.963	4.574
25	BB29	Sprat	12.5	12.3	*	*	-21.480	9.389	16.983	4.889
25	BB29	Sprat	11.0	9.1	*	*	-21.438	9.099	16.706	5.179
25	BB29	Sprat	11.5	12.2	*	*	-21.175	9.211	16.692	5.098
25	BB29	Sprat	10.0	7.0	*	*	-22.333	9.750	17.300	4.178
25	BB29	Sprat	12.5	12.0	*	*	-22.135	9.767	17.065	4.001
25	BB29	Sprat	10.0	7.0	*	*	-21.589	8.977	16.682	4.299
25	BB29	Sprat	10.5	7.8	*	*	-21.272	9.278	16.774	4.441
25	BB29	Sprat	13.0	13.5	*	*	-22.708	9.998	17.051	4.109
25	BB29	Sprat	11.0	8.2	*	*	-21.645	9.511	17.254	3.969
26	GD57	Sprat	12.5	12.5	*	*	-21.282	9.141	16.911	4.370
26	GD57	Sprat	9.5	6.5	*	*	-21.769	9.883	17.001	4.770
26	GD57	Sprat	11.5	9.6	*	*	-22.105	9.626	16.915	4.132

26	GD57	Sprat	10.5	6.9	*	*	-22.419	9.203	17.283	4.554
26	GD57	Sprat	11.5	9.9	*	*	-22.768	9.333	17.350	4.222
26	GD57	Sprat	11.0	8.3	*	*	-22.533	11.766	16.809	4.877
26	GD57	Sprat	10.5	7.0	*	*	-21.386	10.303	17.765	4.155
26	GD59	Sprat	8.5	4.8	*	*	-21.491	9.471	17.127	4.256
26	GD59	Sprat	10.5	8.6	*	*	-22.053	8.843	17.057	4.301
25	BB29	Three-spined stickleback	6.0	2.4	*	*	-22.199	9.892	18.501	4.524
25	BB29	Three-spined stickleback	5.5	2.0	*	*	-21.940	10.492	18.468	4.237
25	BB29	Three-spined stickleback	5.0	1.3	*	*	-21.988	9.995	18.232	4.270
25	BB29	Three-spined stickleback	6.5	2.4	*	*	-21.541	9.412	18.330	4.558
25	BB29	Three-spined stickleback	3.5	0.4	*	*	-21.988	9.774	18.405	5.134
25	BB29	Three-spined stickleback	4.0	0.6	*	*	-21.625	10.309	18.118	4.624
25	BB29	Three-spined stickleback	4.5	1.1	*	*	-21.619	10.269	18.013	4.576
25	BB29	Three-spined stickleback	6.0	2.2	*	*	-21.820	9.909	18.679	4.410
25	BB29	Three-spined stickleback	6.0	1.9	*	*	-21.718	10.270	18.801	4.684
24	H24	Turbot	20.0	140.0	*	*	-19.976	11.163	16.927	4.110
22	KB06	Whiting	25.0	111.0	*	*	-20.974	14.322	13.876	3.988
22	KB06	Whiting	17.0	35.0	*	*	-21.712	14.357	12.040	4.038
22	KB06	Whiting	17.0	35.0	*	*	-19.736	14.381	12.949	3.898
22	KB06	Whiting	7.4	4.0	*	*	-20.534	16.175	16.690	4.125
22	KB06	Whiting	10.3	9.9	*	*	-21.203	15.366	16.356	4.191
22	KB06	Whiting	11.8	11.7	*	*	-20.948	15.442	16.588	4.085
24	H19	Whiting	33.0	393.0	*	*	-20.997	13.699	16.245	3.974
24	H19	Whiting	28.0	194.0	*	*	-21.356	13.762	15.005	3.980
24	H19	Whiting	38.0	459.0	*	*	-20.910	13.574	17.027	3.998
24	H19	Whiting	35.0	405.0	*	*	-20.908	13.696	16.744	3.891
24	H19	Whiting	29.0	221.0	*	*	-19.506	12.991	13.306	4.052
24	H19	Whiting	32.0	224.0	*	*	-21.493	13.734	16.656	3.970
24	H19	Whiting	27.0	163.0	*	*	-20.833	13.240	14.206	4.035

24	H19	Whiting	25.0	133.0	*	*	-20.594	13.500	13.534	3.915
24	H19	Whiting	30.0	202.0	*	*	-21.058	13.138	16.757	3.984
24	H19	Whiting	31.0	256.0	*	*	-20.444	13.634	15.716	4.082
25	BB05	Whiting	32.0	266.0	*	*	-20.963	12.693	17.647	3.933
25	BB05	Whiting	35.0	332.0	*	*	-21.263	13.239	16.822	3.935
25	BB05	Whiting	32.0	300.0	*	*	-19.589	13.777	16.137	3.886
25	BB05	Whiting	31.0	264.0	*	*	-20.037	13.358	15.649	4.030
25	BB17	Whiting	32.0	261.0	*	*	-20.284	12.691	17.062	4.002
25	BB35	Whiting	22.0	85.0	*	*	-18.970	12.830	15.385	4.078
25	BB39	Whiting	20.0	60.0	*	*	-20.947	12.532	16.556	4.003

Appendix 2.3. Summary of results of ANCOVA general linear model (GLM) of cod (n=61) and whiting (n=17), with $\delta^{13}C$ as response variable, SD, species and SD*species as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=6.74%. SD24 – Arkona Basin, SD25 – Bornholm Basin.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	0.0002	0.0354	0.0354	0.13	0.723
SD	1	0.0004	0.4077	0.4077	1.46	0.231
species	1	0.0537	0.0148	0.0148	0.05	0.819
SD*species	1	1.4195	1.4195	1.4195	5.08	0.027
Error	73	20.4079	20.4079	0.2796		
Total	77	21.8817				

Appendix 2.4. Summary of results of ANCOVA general linear model (GLM) of cod (n=61) and whiting (n=17), with $\delta^{15}N$ as response variable, SD, species and SD*species as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=31.20%. SD24 – Arkona Basin, SD25 – Bornholm Basin.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	0.6755	0.0141	0.0141	0.04	0.837
SD	1	9.4540	5.2663	5.2663	16.03	<0.001
species	1	0.4008	0.3325	0.3325	1.01	0.318
SD*species	1	0.3459	0.3459	0.3459	1.05	0.308
Error	73	23.9784	23.9784	0.3285		
Total	77	34.8547				

Appendix 2.5. Summary of results of ANOVA general linear model (GLM) of herring (n=10), sprat (n=10) and three-spined stickleback (n=9), with $\delta^{15}N$ as response variable, and species as explanatory variables. Overall variability explained by the model was R^2=59.63%. SD25 – Bornholm Basin.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
species	2	9.7173	9.7173	4.8587	19.20	<0.001
Error	26	6.5785	6.5785	0.2530		
Total	28	16.2958				

Appendix 2.6. Summary of results of ANOVA general linear model (GLM) of herring (n=10), sprat (n=10) and three-spined stickleback (n=9), with $\delta^{13}C$ as response variable, and species as explanatory variables. Overall variability explained by the model was R^2=9.0%. SD25 – Bornholm Basin.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
species	2	0.6255	0.6255	0.3127	1.29	0.293
Error	26	6.3216	6.3216	0.2431		
Total	28	6.9471				

Appendix 2.7. Summary of results of ANCOVA general linear model (GLM) of dab (n=10), flounder (n=9) and plaice (n=7), with $\delta^{13}C$ as response variable, species and species*TL as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=55.42%. SD22 – Kiel Bight.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	1.1074	2.1882	2.1882	6.61	0.018
Species	2	3.3656	3.6802	1.8401	5.56	0.012
species*TL	2	3.7558	3.7558	1.8779	5.67	0.011
Error	20	6.6191	6.6191	0.3310		
Total	25	14.8479				

Appendix 2.8. Summary of results of ANCOVA general linear model (GLM) of dab (n=10), flounder (n=9) and plaice (n=7), with $\delta^{15}N$ as response variable, species and species*TL as explanatory variables, and TL as covariate. Overall variability explained by the model was R^2=21.68%. SD22 – Kiel Bight.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
TL	1	0.3905	0.2550	0.2550	0.61	0.446
Species	2	1.8563	0.2481	0.1241	0.29	0.748
species*TL	2	0.0828	0.0828	0.0414	0.10	0.907
Error	20	8.4181	8.4181	0.4209		
Total	25	10.7476				

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DECLARATION OF AUTHORSHIP

I hereby declare that the present thesis is my own work and that I have not used other than the stated sources and aids.

The submitted written version corresponds to the electronic one.

I further assure that this thesis has not been previously presented to any other examination board and has not been published.

Place/Date Signature